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ON ALTERNATIVE REPRODUCTIVE TACTICS IN ANURANS: DYNAMIC GAMES WITH DENSITY AND FREQUENCY DEPENDENCE

JEFFREY R. LUCAS AND RICHARD D. HOWARD

Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907

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Abstract.—Intense mating competition and mate choice has favored the evolution of alternative mating tactics in many species. We developed a stochastic dynamic game to evaluate the choice among three alternative mating tactics by male anurans: call, satellite, or leave the chorus to forage or hide. The strategies were assumed to differ in mating success (call > satellite > forage = hide), predation risk (call > satellite > forage > hide), and energetic expense (call > satellite = hide > forage). Six major predictions were derived. First, in relatively stable environments, males should enter a chorus in a synchronous pulsed pattern, with first-year males primarily choosing to be satellites on older calling males. The pulsed pattern is caused by the relatively high energetic cost of calling and the dependence of female arrival rates on chorus size (which promotes synchronization). In unstable environments, energetic constraints are reduced because favorable conditions are rare, so most males should call on favorable nights. Under all conditions, energy-constrained males should forage. Second, with an accelerating relationship between female arrival rate (measured per calling male) and chorus size, first-year males in a stable environment should drop out of choruses before the end of the breeding season because the payoff to attendance decreases as the population declines; with a decelerating function, first-year males should remain the entire year. In an unstable environment, males should enter a chorus on favorable days, irrespective of the shape of the female arrival function. Third, variation in the form of predation risk with respect to chorus size has little or no effect on mating patterns; however, high mean predation risk should increase the frequency of satellites in the chorus. Fourth, conflicts can occur between old males that are selected to call and young males that are selected to act as satellites. Under some conditions, the only resolution to this conflict is for all males to abandon the chorus. Fifth, if there are differences among first-year males in when they come into breeding condition, the few males that mature early should be satellites. Later in the season, first-year males should tend to call. This prediction is unaffected by density dependence in predation risk, but it does not hold when female arrival rate is density-independent. Finally, first-year males should call more when their mating success decreases with an increase in the number of calling older males in comparison with conditions in which mating success is a fixed fraction of the mating success of older males. We show that the properties of a number of anuran species make them amenable to test these predictions.

Males expend an extraordinary amount of energy to obtain mates in a number of animal species (see, e.g., Clutton-Brock et al. 1979; Halliday 1987; Grafen 1990). Elephant seals, white-faced dragonflies, and bullfrogs set up and defend territories in high-quality habitats, field crickets and ruffs advertise from leks, and red deer and gazelle defend moving groups of females. One striking similarity of these species is that some males forgo the costs and risks of advertisement and territory or female defense and instead employ any one of several forms of low-cost alternative mating tactics (Rubenstein 1980; Dunbar 1982). To under-

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stand the evolutionary maintenance of a diversity of male mating tactics, we need to understand two general phenomena: mechanisms that generate the expression of these traits (e.g., Are they genetically determined or conditional on the current state of the male?) and factors that influence the reproductive payoffs to each mating tactic.

In some species, alternative tactics appear either to have a strong genetic base or to be irreversibly triggered early in development (see, e.g., Cade 1981; Gross 1984); however, in many species, alternative tactics can be employed by any male in the population, and their use is governed by a male's current state (Rubenstein 1980; Greenfield and Shelly 1985; Arak 1988*a*). We address only the latter group here. We consider conditions that regulate payoffs to alternative tactics and how these conditions affect the evolutionary stability of male mating behaviors.

Vehrencamp and Bradbury (1984) distinguish three generations of studies on the evolutionary aspects of mating systems. First-generation studies look for correlations and devise post hoc scenarios that would explain observed patterns. Second-generation studies evaluate specific fitness components and compare observed patterns with patterns expected from the maximization of these components. Third-generation studies have only recently begun and incorporate multiple fitness components concurrently. Previous models of the evolution of alternative mating tactics (see, e.g., Rubenstein 1980; Waltz 1982; Fairchild 1984; Arak 1988*a;* Woolbright et al. 1990) could be categorized as second-generation models. Each focuses on a narrow range of fitness components (see Discussion for a review of some of these models). While these models underscore the need to consider specific fitness components, a third-generation model is necessary to understand how fitness components interact to maintain alternative mating tactics in any given population. We used stochastic dynamic game theory (Mangel and Clark 1988) to provide a framework for such a third-generation model.

We concentrate on anuran caller and satellite tactics to illustrate some of the complexities in alternative mating tactics. Mating behavior can vary both within and among species; we address both levels of variation. We ask under what conditions within-population variation could reflect temporal changes in behavior (e.g., variation between mating tactics chosen early in the breeding season and those chosen late in the season) or differences between individuals in energetic state, age, or reproductive potential. We then vary specific parameter values or functions to reflect differences between species. This approach should provide insight into the causal mechanisms maintaining the diversity of male reproductive tactics. We focus primarily on anuran species because male mating tactics have been particularly well characterized in this group; however, a number of the conclusions of this model are likely to hold for other groups (notably, many Orthoptera with mating systems similar to anurans), and the model can be modified for other taxa.

Our model is designed to reflect the general characteristics of anuran mating behavior. Anuran mating behavior, like many other behaviors, is fundamentally a dynamic game. It is dynamic because the payoffs to any behavior may vary with the physiological state of an individual, which in turn influences its future state and future decisions (Clark 1991). For example, energy stores influence a number of reproductive functions, including the fecundity (Crump 1974) and mating tactics of males (Taigen and Wells 1985; Given 1988*a;* Grafe et al. 1992). In addition, females may often base mate choice on male acoustical signals that are energetically expensive to produce (see, e.g., Ryan 1988; Gerhardt 1991). Anuran mating behavior is a game because the fitness payoffs to any behavior will depend, in part, on the behaviors of other individuals in the population. These relationships can act in either a frequency- or density-dependent manner. Previous behavioral studies have typically evaluated only frequency-dependent games (e.g., Lande 1981; Maynard Smith 1982), although some density-dependent attributes of behavior have recently been addressed (Vickery et al. 1991; Read and Harvey 1993; Crowley and Hopper 1994). Anuran mating behavior is an ideal model system for an expanded version of dynamic game theory because reproductive payoffs to males are demonstrably density-dependent (see, e.g., Howard 1984; Hoglund and Robertson 1988; Sullivan 1989) and are likely to be frequency-dependent as well (Arak 1988*a*). Unfortunately, frequency- and density-dependent games are often quite complicated. However, for behaviors that are by nature dynamic games, we need to understand the theoretical consequences of this complexity.

Here we extend our initial model of anuran mating behavior (Lucas et al., in press) to examine factors that govern seasonal patterns in mating behavior. Our model focuses specifically on the relationships between callers and satellites. The model incorporates five critical properties of anuran mating decisions.

Physiological state dependence.—Male mating decisions are potentially affected by the energetic costs of mating behavior, by the initial energy reserves of males, and by the ability of males to recoup energetic losses by foraging during the mating season (see, e.g., Wells 1978; Cherry 1993).

Male density-dependent female arrival rates.—In several species, the number of calling males in a chorus is correlated with female arrival rates per caller (see, e.g., Ryan et al. 1981; Tejedo 1992; Wagner and Sullivan 1992). This correlation could result from females responding preferentially to large choruses (Wells 1977*a*), in which case female arrival rates are caller density-dependent. This density dependence could be generated (or exacerbated) if females choose among choruses on the basis of some aspect of overall sound level generated by the chorus. Alternatively, this correlation could result indirectly if both males and females used the same environmental cues to decide when to enter a breeding area, but females require a stronger cue than males. The result would be a small chorus on nights when females do not arrive and a large chorus when female arrival rate is maximal (Ritke et al. 1992; Wagner and Sullivan 1992). Under these conditions, female arrival rates would be independent of male density.

Male density-dependent predation risk.—Predation risk per male in a chorus can be a function of male density (Ryan et al. 1981; Jennions and Backwell 1992).

Satellite frequency-dependent mating success.—Satellites intercept females attracted by calling males (Wells 1977*a;* Howard 1978; Perrill et al. 1978) and thereby lower the mating success of callers. Thus, caller mating success could be influenced by the frequency of satellites in the chorus. In addition, if female arrival rate is a function of the number of calling males (Wells 1977*a*), males that choose to become (silent) satellites instead of calling effectively reduce chorus size and thereby reduce female arrival rate.

Age-dependent mating success.—Young males may have lower mating success than old males as a result of reduced success in mate competition and/or mate choice (see, e.g., Howard 1978, 1984). Unfortunately, data on age-related differences in mating success are unavailable for most species, so the degree to which this trend generalizes across species is unknown. Age differences in behavior and level of chorus attendance (which often correlates with mating success) are also not available for most species. As a result, inferences of age-dependent variation in mating success must be indirect: although the relationship between male body size and age is relatively weak in most anurans (Halliday and Verrell 1988), the most pronounced size difference among males is between first-year breeders and older breeders (see, e.g., Lykens and Forester 1987; Platz and Lathrop 1993; Howard et al. 1994). In addition, body size influences mating success in many (see, e.g., Arak 1983; Sullivan 1983; Verrell 1983; Howard and Kluge 1985), but not all (Gerhardt et al. 1987), anuran species. Thus, we assume here that first-year males will have a reduced expectation of mating success relative to that of old males on the basis of either size differences or some other correlate of age.

Temporal patterns in mating behavior in anuran choruses vary considerably among species. In some species, males are more likely to be satellites early in the mating season (Garton and Brandon 1975; Howard 1984); in others, the frequency of satellites is highest at both the beginning and end of the breeding season (Roble 1985); in others, no temporal pattern can be discerned (Lykens and Forester 1987). Numerous factors undoubtedly underlie this variation. In a related article (Lucas et al., in press), we show that the energetic costs to calling males, the maximum length of the breeding season, the magnitude of predation risk to males in the chorus, and the efficiency with which satellites intercept females will all affect the equilibrium composition of the chorus. In this article, we explore five additional potential sources of this variation: the stability of the breeding environment (i.e., the number of days on which female arrival rates are high as a result of local environmental conditions), the effect of chorus size on female arrival rate into a calling male's territory, the density-dependent predation risk, the seasonal variation in the number of reproductive first-year males, and the seasonal variation in the mating success of young males caused by variation in the number of competing old males. Below, we describe a dynamic game that allows us to evaluate the simultaneous effect of each of these factors on the mating decisions of male anurans. We then show how changes in these factors should govern reproductive decisions. Finally, we discuss species in which these predictions can be tested.

THE MODEL

We model male anuran mating decisions as a stochastic dynamic game, using an algorithm suggested by Houston and McNamara (1987, 1988; see Mangel 1990 for a discussion of the technique). We will first briefly outline the model, then discuss each part of the model in detail.

Males are assumed to choose among four different behaviors: call, satellite, forage, and hide. The latter two behaviors are performed away from the chorus, and the first two are performed in the chorus. We assume that the decision is made once per day and commits the male to a given course of action for a full day. Each decision is assumed to result in a specified change in energy reserves (i.e., energy is the state variable) and predation risk. Energetic expenditure, and therefore starvation risk, is assumed to be highest for calling males and lowest for hiding males. For males in the chorus, predation risk is assumed to decrease with chorus size; predation risk is also assumed to be generally higher for males in the chorus than for foraging or hiding males.

The choice among behaviors is assumed to be based on lifetime mating success. Male mating success is assumed to be a function of the mating tactic chosen by a male, the degree of competition between males, male age, and the arrival rate of females into the chorus. Female arrival rate, in turn, is a function of day in the breeding season, environmental quality (e.g., amount of precipitation), and size and composition of the chorus. We simplify male age to allow for two age categories, first-year males (males in their first year after sexual maturation) and second-year males (males returning to breed in their second year of adulthood).

We seek a state- and time-dependent strategy that is evolutionarily stable, or resistant to invasion by a mutant strategy. The algorithm we used to find the evolutionarily stable strategy (ESS) has two parts: a backward iteration (or dynamic program) and a forward iteration (or simulation). We start with some initial guess about the number of callers and satellites of each age class on each night of the season. We then use stochastic dynamic programming (Mangel and Clark 1988) to find the best strategy (i.e., the one that maximizes lifetime mating success) that a single male should play against this population. The dynamic program essentially identifies the best mutant strategy that could invade the population. The optimal strategy is calculated for all possible combinations of environmental state, energetic state, day in the season, and male age. We then use a simulation to determine the composition of a chorus composed entirely of these mutants. This two-part process is then repeated until the best mutant strategy is identical with the strategy shown by the rest of the population. This strategy is the evolutionarily stable strategy (Parker 1984; or more specifically, the Nash equilibrium)—that is, the strategy that, when played by the entire population, does not allow invasion by a single mutant playing some alternative strategy.

It usually takes between five and 10 iterations for the algorithm to find the ESS, when one exists. However, there are conditions in which no ESS is found (see Houston and McNamara 1987; Lucas et al., in press). In these cases, we present the results of the model after 50 iterations.

The dynamic program solves for the best mutant strategy by assuming that expected lifetime reproductive success (LRS) is maximized. The mutant's LRS, in turn, is affected by survival rate and mating success.

Survival Rate

Starvation rate on any night during the breeding season is taken as a function of the level of energetic reserves and is modeled by means of an incomplete beta function (I). (Throughout this article, square brackets indicate that the variable

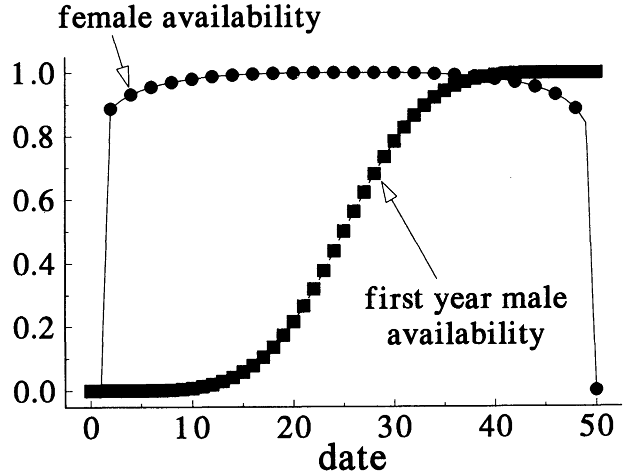

FIG. 1.—Functions used in the model for availability of females (*solid circles*, see eq. [5]) and first-year males (*solid squares*, see eq. [15]) over the course of the mating season. Both variables are given as a fraction of the maximum number of anurans.

is a function of the bracketed terms.) Thus,

$$\mu_{st}[e] = 1 - I_e(a_e, b_e), \qquad (1)$$

where $\mu_{st}[e]$ is the starvation rate per night (a function of energy state e) and $I_e(a_e, b_e)$ is an incomplete beta function of relative energy state e with arguments a_e and b_e. The incomplete beta function is a cumulative distribution function of some variable ranging from zero (at $e = 0$) to one (at $e = 1$). Here, e is the fraction of maximal energy reserves carried by a male at the beginning of any given night. The incomplete beta function is similar in shape to a cumulative normal distribution, except that it has the biological realism of finite tails (*first year male availability* in fig. 1, for example).

To run the dynamic program, energetic state and time are divided into discrete intervals. Time is broken into intervals of 1 d. We divide energetic state into a series of 30 intervals and assume that the result of each chosen behavior is a stochastic change in state. Thus, if the current state is ϵ (which ranges from zero to 30), then $\Delta\epsilon_i \pm \sigma_{\epsilon i}$ is the per-day change in state caused by the choice of behavior i. We assume a normal frequency distribution of energy states for each age class of males in the population on the first day of the mating season, with $\mu = 25.5$ and $\sigma^2 = 2.86$. (This is relevant only for the forward iteration.)

We assume that overwinter mortality ($\mu_{ow}[e]$, the probability of dying at any time from the end of one breeding season until the beginning of the next breeding season) is also a function of the energetic state of a male at the end of the season such that

$$\mu_{ow}[e] = 1 - I_e(a_{ow}, b_{ow}) \times \gamma_{ow}, \qquad (2)$$

where $I_e(a_{ow}, b_{ow})$ is the incomplete beta function for overwinter mortality and γ_{ow} is the maximum overwinter survival rate.

Predation rate in a chorus (μ_{call}[date, rd], where "date" is the number of days since the breeding season started, and "rd" is the variable representing environmental quality, arbitrarily called rain days) is assumed to vary as a function of chorus size and satellite frequency; thus,

$$\mu_{\text{call}}[\text{date, rd}] = \frac{\beta_p \times (1 - C[\text{date, rd}])}{1 + \beta_{\text{sat}} \times \dfrac{S[\text{date, rd}]}{C[\text{date, rd}]}}, \tag{3}$$

where β_p is the maximum probability of a predation event in a territory in one night during the breeding season, β_{sat} is the satellite mortality rate divided by the caller mortality rate, C[date, rd] is the relative number of calling males, and S[date, rd] is the relative number of satellites. This relationship assumes that predators locate callers either acoustically or by means of movement cues and thus primarily cue on signals emitted by the caller (see, e.g., Howard 1978; Ryan et al. 1981; Perrill and Magier 1988). The relative number of calling males on any given day of the breeding season is taken as a fraction of the maximal possible number of males (i.e., the number of males with 100% survival rate), assuming environmental quality rd. Thus, C[date, rd] reflects both a reduction in chorus size caused by mortality and the proportion of males in the chorus that are calling. The numerator in equation (3), the probability of a predation event in a calling male's territory, is assumed to be a linear function of chorus size. The denominator accounts for the fact that satellites can share the risk of predation. We assume that $\beta_s < 1$. The denominator, therefore, is the effective number of individuals that can be preyed on in a territory. The reciprocal of this number is the probability that the caller is killed when an attack occurs. The predation risk to a satellite in the territory (μ_{sat}[date, rd]) is taken as a fraction of the risk to callers, which gives

$$\mu_{\text{sat}}[\text{date, rd}] = \beta_{\text{sat}} \times \mu_{\text{call}}[\text{date, rd}]\,. \tag{4}$$

We assume that the probabilities that a forager is killed in one day (μ_{forage}) and that a male in a refuge is killed in one day (μ_{hide}) are lower than those for males in a chorus, and that both μ_{forage} and μ_{hide} are constant.

Mating Success

There are two components to LRS, the mating success on a given night (current mating success) and the expected future reproductive success. Current mating success, which is nonzero only for callers and satellites, is a function of three variables: time in season, environmental quality, and chorus size. For simplicity, we assume that lifetime mating success is equivalent to LRS. In species in which the size and survival rate of clutches varies seasonally (see, e.g., Morin et al. 1990), this part of the model would have to be altered to include the seasonally adjusted value of a mating. Our model could also be easily extended to adjust the value of matings for phenomena such as size-assortative mating, for which there is a higher fitness payoff per mating for larger males.

The seasonal female-availability function assumes that there is some maximum number of females that could potentially arrive on a given day in the breeding season. This number increases through the first part of the year, decreases thereafter, and is modeled with concatenated incomplete beta functions of the day in season (*female availability,* fig. 1). Thus,

$$\Phi[\text{date}] = \begin{cases} I_{\tau1}(a_\sigma, b_\sigma) & \text{if date} < T_{\max}/2 \\ I_{\tau2}(a_\sigma, b_\sigma) & \text{otherwise}, \end{cases} \tag{5}$$

where Φ[date] is the seasonal component of female availability, $I_{\tau1}(a_\sigma, b_\sigma)$ and $I_{\tau2}(a_\sigma, b_\sigma)$ are incomplete beta functions for female arrival rate (where $\tau1 = 2 \times \text{date}/T_{\max}$, $\tau2 = 2 \times [1 - \text{date}/T_{\max}]$, and a_σ and b_σ are arguments of the incomplete beta function), and $T_{\max}$ is the maximum length of the breeding season.

In many species, female arrival rates are correlated with environmental variables such as rainfall or temperature, with females typically arriving on warm, rainy evenings (see, e.g., Robertson 1986; Telford and Dyson 1990; Ritke et al. 1992; Tejedo 1992). (Note that in all cases, our measure of female arrival rate is the rate per calling male.) We combine these environmental variables into the single variable rd and assume that female arrival rate is a linear function of environmental quality. Thus,

$$\rho[\text{rd}] = \begin{cases} 1 - \text{rd}/4 & \text{if rd} \leq 4 \\ 0 & \text{otherwise}, \end{cases} \tag{6}$$

where ρ[rd] is the environmental component of female availability. The value of rd ranges from zero (highest quality) to four (lowest quality). We assume that rd increases in increments of one (when rd < 4, and by zero otherwise) with some fixed probability, $1 - \text{P}_{\text{rain}}$, on each day of the breeding season and reverts to rd = 0 with a probability of P_{rain}. This is analogous to rain immediately increasing the availability of females and to female arrival rate decreasing with the number of days since the last rain. We will call high-quality days (i.e., days when rd = 0) rainy days, although rain is meant to correspond to the suite of environmental factors that promote high female arrival rates into the chorus. Most of the chorus activity occurs on favorable days (i.e., low rd); therefore, to simplify the discussion of the model results, we only present results from favorable days.

Finally, we assume that the arrival rate of females into a male's territory increases with chorus size. Thus,

$$\xi[\text{date}, \text{rd}] = \gamma_{\xi1} \times (C[\text{date}, \text{rd}] \times 2 + \gamma_{\xi2} \times C[\text{date}, \text{rd}]^2), \quad . \tag{7}$$

where ξ[date, rd] is the chorus-size component of female availability, $\gamma_{\xi1}$ is the maximum female arrival rate, and $\gamma_{\xi2}$, a constant, is a coefficient determining the shape of the relationship between female arrival rate and chorus size. If $\gamma_{\xi2}$ is positive, this function is accelerating (concave up), and if it is negative, the function is decelerating (concave down; see fig. 2*A*). If there are no calling males in the population, we assume that a mutant (and lone) caller represents a relative chorus size of 10^{-4}.

The net female arrival rate (F[date, rd]) into an average caller's territory is

$$F[\text{date}, \text{rd}] = \xi[\text{date}, \text{red}] \times \rho[\text{rd}] \times \Phi[\text{date}]. \tag{8}$$

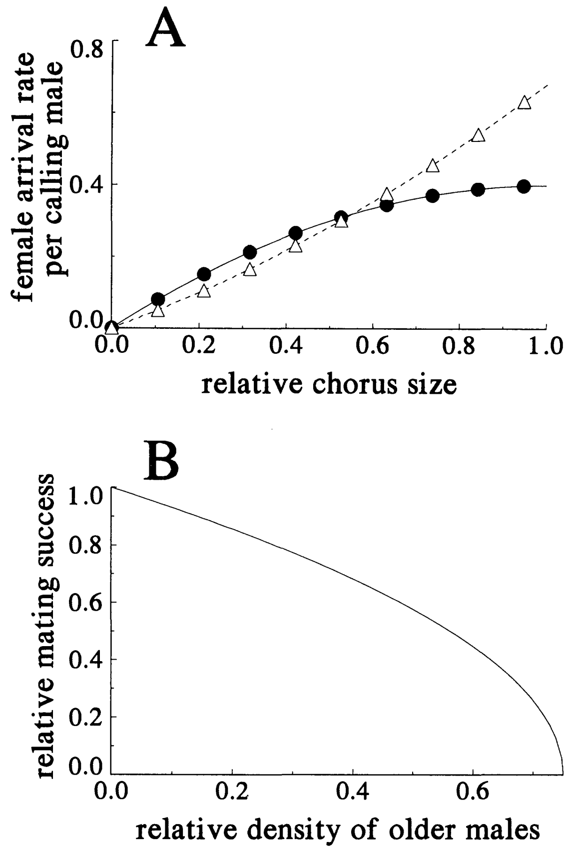

FIG. 2.—*A*, Chorus-size-dependent female arrival rate functions used in model (see eq. [7]). *Open triangles*, accelerating function ($\gamma_{\xi 1} = 0.227$; $\gamma_{\xi 2} = 1$); *solid circles*, decelerating function ($\gamma_{\xi 1} = 0.4$; $\gamma_{\xi 1} = -1$). *B*, Relationship used in model between mating success of first-year males and relative density of second-year males (see eq. [16]).

This is the average female arrival rate across all territories. However, young males may experience a lower mating success than old males. For simplicity, we will assume that the net effect of this age difference is that young males attract fewer females into their territories than old males, and we subsume any type of competition for mates into this age effect. The age difference can be accounted for in the following manner.

Assume that any given first-year male is able to attract some fraction of the number of females a second-year male will attract (γ_1), and assume that p_1[date] is the proportion of callers that are first-year males; old males will attract females at a rate

$$v_2[\text{date}, \text{rd}] = \frac{F[\text{date}, \text{rd}]}{1 - p_1[\text{date}]\,(1 - \gamma_1)}, \tag{9}$$

where ν_2[date, rd] is the rate at which old males attract females, and ν_1 [date, rd] is the rate at which first-year males will attract females, such that

$$\nu_1[\text{date}, \text{rd}] = \nu_2[\text{date}, \text{rd}) \times \gamma_1 . \tag{10}$$

In addition to age, the frequency of satellites in the chorus will affect mating rates. This is because females arriving in the territory are shared among the caller and satellites in the territory; thus, the current mating success of the caller is the rate at which females are attracted to the territory on a given night of the season, diminished by the rate at which satellites intercept females. Thus,

$$\text{MS}_{\text{call}}[\text{age}, \text{date}, \text{rd}] = \frac{\nu_{\text{age}}[\text{date}, \text{rd}]}{1 + \gamma_{\text{sat}} \times \dfrac{S[\text{date}, \text{rd}]}{C[\text{date}, \text{rd}]}}, \tag{11}$$

where MS_{call}[age, date, rd] is the current mating success of a caller, ν_{age}[date, rd] is the rate at which males of the age "age" attract females, and γ_{sat} is the ability of a single satellite to obtain mates taken as a fraction of the ability of a caller to obtain mates. (We assume that $\gamma_{\text{sat}} < 1$.)

The current mating success of a satellite (MS_{sat}[age, date, rd]) is assumed to be age-independent:

$$\text{MS}_{\text{sat}}[\text{age}, \text{date}, \text{rd}] = \frac{F[\text{date}, \text{rd}] \times \gamma_{\text{sat}}}{1 + \gamma_{\text{sat}} \times \dfrac{S[\text{date}, \text{rd}]}{C[\text{date}, \text{rd}]}}. \tag{12}$$

The current mating success of foraging males ($\text{MS}_{\text{forage}}$[age, date, rd]) and hiding males MS_{hide}[age, date, rd]) is zero:

$$\text{MS}_{\text{forage}}[\text{age}, \text{date}, \text{rd}] = \text{MS}_{\text{hide}}[\text{age}, \text{date}, \text{rd}] = 0 . \tag{13}$$

Total Lifetime Reproductive Success

The total reproductive payoff of a male (PO_{behav}[age, date, rd, ϵ]) equals current mating success plus expected future reproductive success, which gives

$$\begin{aligned}
&PO_{\text{behav}}[\text{age}, \text{date}, \text{rd}, \epsilon] \\
&= \text{MS}_{\text{behav}}[\text{age}, \text{date}, \text{rd}] + (1 - \mu_{\text{st}}[\epsilon]) \times (1 - \mu_{\text{behav}}[\text{date}, \text{rd}]) \\
&\times \Bigg(\text{P}_{\text{rain}} \times \Bigg\{\text{P}_c \times \Bigg(\sum_{\Delta\epsilon = -30}^{30} \text{P}_{\Delta\epsilon|\text{behav}} \times PO^*[\text{age}, \text{date} + 1, \text{rd} = 0, \epsilon + \Delta\epsilon]\Bigg) \\
&\quad + (1 - \text{P}_c) \times \Bigg(\sum_{\Delta\epsilon = -30}^{30} \text{P}_{\Delta\epsilon|\text{behav}} \times PO^*[\text{age}, T_{\max} + 1, \text{rd} = 0, \epsilon + \Delta\epsilon]\Bigg)\Bigg\} \\
&\quad + (1 - \text{P}_{\text{rain}}) \times \Bigg\{\text{P}_c + \Bigg(\sum_{\Delta\epsilon = -30}^{30} \text{P}_{\Delta\epsilon|\text{behav}} \times PO^*[\text{age}, \text{date} + 1, \text{rd} + 1, \epsilon + \Delta\epsilon]\Bigg) \\
&\quad + (1 - \text{P}_c) \times \Bigg(\sum_{\Delta\epsilon = -30}^{30} \text{P}_{\Delta\epsilon|\text{behav}} \times PO^*[\text{age}, T_{\max} + 1, \text{rd} + 1, \epsilon + \Delta\epsilon]\Bigg)\Bigg\}\Bigg),
\end{aligned} \tag{14}$$

where MS_{behav}[age, date, rd] is the current payoff if the male exhibits the behavior "behav," $\mu_{st}[\epsilon]$ is the probability of starvation per day as a function of energy state ϵ, μ_{behav}[date, rd] is the mortality risk of the behavior behav, P_c is the probability that the mating season will continue at least another day, $P_{\Delta\epsilon|behav}$ is the probability that energetic state is changed by $\Delta\epsilon$ given that behavior behav is exhibited, PO^* is the optimal payoff for the sequence of decisions made for the rest of the male's life starting on day = date + 1 (if the season lasts that long) or day = $T_{max} + 1$ (if the season ends), on rd = 0 (if it rains) or rd + 1 (if it does not rain), and at energy state $\epsilon + \Delta\epsilon$.

Changing Densities of First-Year Males and Competition between Age Classes

The above model makes two important assumptions about first-year males: that first-year males are reproductively competent at the beginning of the breeding season and that their mating success is independent of the number of old males in the chorus. Each of these assumptions is likely to be violated, at least in some species. For example, in several species of anurans, some young males may not be sexually mature at the beginning of the reproductive season, or they may not possess the energetic stores required to enter the breeding population; these males may enter the chorus only after the beginning of the breeding season, which causes a decrease in mean age or size of males in the chorus (Gatz 1981; Howard 1981; Sullivan 1987). Also, in species such as bullfrogs (*Rana catesbeiana*), yearling males may be less successful at obtaining mates when the number of old males is high (Howard 1984).

To evaluate the impact of these assumptions on the predictions of the model, we alter the following relationships: Let the proportion of first-year males that are capable of joining the chorus increase during the course of the breeding season. We assume that this proportion increases monotonically over the breeding season and model it with an incomplete beta function ($I_{\delta B}(a_B, b_B)$; see fig. 1), which gives

$$B[\text{date}] = I_{\delta B}(a_B, b_B)\,, \tag{15}$$

where B[date] is the proportion of first-year males capable of joining the chorus, δB equals date/T_{max}, and a_B and b_B are arguments for the incomplete beta function that relate the fraction of first-year males that are reproductively competent to the day in the season. First-year males that are not able to join the chorus are assumed to forage.

Let the old males in the chorus affect the mating success of young males (Γ_1[date]). This is modeled by

$$\Gamma_1[\text{date}] = (1 - C_2[\text{date, rd}] \times \beta_1)^{\beta\Gamma}\,, \tag{16}$$

where C_2[date, rd] is the number of second-year breeders taken as a fraction of the number of males of that cohort that were alive on the first day of their first reproductive season. The number of first-year males displaced from calling sites by each second-year male is given by β_1; this is arbitrarily taken as $1/\gamma_{ow}$ (see above). The shape of the function is determined by β_{Γ}; this is illustrated in figure 2*B*.

The Basic Model

We start with an initial set of assumptions in the basic model, then evaluate how modification of these assumptions affects the predicted behaviors. The results of each game can be described in terms of the number of males exhibiting each behavior pattern, the individual decision matrix (i.e., the decisions each male should make as a function of its energetic state, environmental quality, and date), or the distribution of energy states of males displaying each of the different behaviors. These perspectives are by definition interdependent, and each provides a complementary understanding of the dynamics of the system. However, to simplify matters, we focus on seasonal patterns in population densities and illustrate the decision matrix and expected population-wide distributions of energy states for a few variations of the basic model.

Precise measurements of the parameter values used in our model are lacking. Thus, we used parameter values inferred from published data. In the basic model, we assume that all first-year males are capable of calling on the first day of the breeding season (see, e.g., Howard 1984). We also assume that first-year males that call attract females at a rate that is 70% that of second-year males ($\gamma_1 = 0.7$) regardless of the density of either age class. Our basic model assumes that female arrival rate (per calling male) increases monotonically with chorus size but with a negative second derivative (i.e., the function is decelerating, with $\gamma_{\xi 2} = -1$). The few descriptions of this relationship in the literature suggest that this relationship varies widely between species (see Discussion). The results from the basic model will then be compared with a model that uses an accelerating function and with a model that assumes that female arrival rate is uncorrelated with chorus size.

It has been hypothesized that energetic constraints limit the number of consecutive days a male can participate in a chorus (Sullivan 1987; Krupa 1989; Murphy 1992; but see Green 1990). In our basic model, the change in energy state for a caller ($\Delta\epsilon_{\text{call}}$) is -2.5 ± 1.4 energy units per night, which means that males with a full energy load can call in a chorus for, on average, 12 consecutive nights without replenishing energy stores. Finally, we assume a fairly stable environment in which female arrival rate is maximal on a majority of nights ($P_{\text{rain}} = 0.8$). See the appendix for a full list of parameter values.

RESULTS

In general, predicted participation in a chorus and the temporal pattern of the chorus are affected by a number of factors. These include environmental stability; the number of males in a chorus, the satellite pressure, and the density-dependent mating payoffs accrued in a chorus; the maturation rate of first-year breeders; and the competitive relationships between age classes. Below, we show

how the predictions from the basic model are altered when each factor is manipulated.

Environmental Stability

Chorus attendance is constrained by the interaction of two factors: environmental stability (P_{rain} is the probability that environmental conditions permit the maximum female arrival rate on any given night) and energetic costs of chorus attendance ($\Delta\epsilon_{call}$ and $\Delta\epsilon_{sat}$; the energetic costs of calling are addressed in Lucas et al., in press). When environmental conditions are favorable (rd = 0), most males are predicted to attend choruses throughout the season, regardless of whether the environment is stable (fig. 3*E* and *F*) or not (fig. 3*A* and *B*). When the expectation of mating success is lower because drier conditions reduce the female arrival rate (e.g., rd = 1), then males are predicted to forage and only attend choruses during the latter part of the mating season, when future mating opportunities approach zero, particularly in environments in which rain is unlikely (cf. fig. 3*C* and *D* with *G* and *H*). However, this general pattern of seasonal chorus attendance may be punctuated by the energetic costs of continued reproductive activity, particularly in calling males (fig. 4*F*). If the daily energetic cost of calling is high, then energy limitations should preclude callers from sustained chorus attendance on rainy days in environments in which most days are likely to be rainy (P_{rain} = 0.8). As a result, a pulsed pattern of chorus attendance should occur for calling males during the breeding season: males with high energy levels call in a chorus for a few days, leave to forage for a day, and then return to call again (fig. 3*E*). These results persist despite variation among males in energy state at the beginning of the breeding season and despite individual variation in resource acquisition (see eqq. [1] and [2]). The pulsed pattern results in part from our assumption that female arrival rates increase monotonically with chorus size. Below, we consider the effect of altering this assumption.

The attendance pattern should be similarly pulsed for young males adopting the satellite strategy, because these males require the presence of calling males for their mating tactic (fig. 3*F*). No such pulsed attendance pattern is expected in environments in which the daily chance of rain is low (P_{rain} = 0.2; fig. 3*A* and *B*), because calling males will have more opportunity to replenish energy stores between rainy days whenever rain occurs during the season (fig. 4*D*).

For both age classes, male behavior should depend on energetic state. Males with low energy stores should primarily forage and not enter choruses; however, low-energy males should be more likely to join choruses on rainy days in environments with infrequent rains than on rainy days in environments with frequent rains (cf. fig. 3*A* and *B* with *E* and *F*). The threshold energy state at which males enter choruses may also vary seasonally. Early in the breeding season, low-energy males are predicted to forage to replenish stores and thereby increase their chorus participation later in the season. In contrast, low-energy males are expected to join choruses later in the season when chances of future mating success are lower.

First- and second-year males should respond differently to variation in environ-

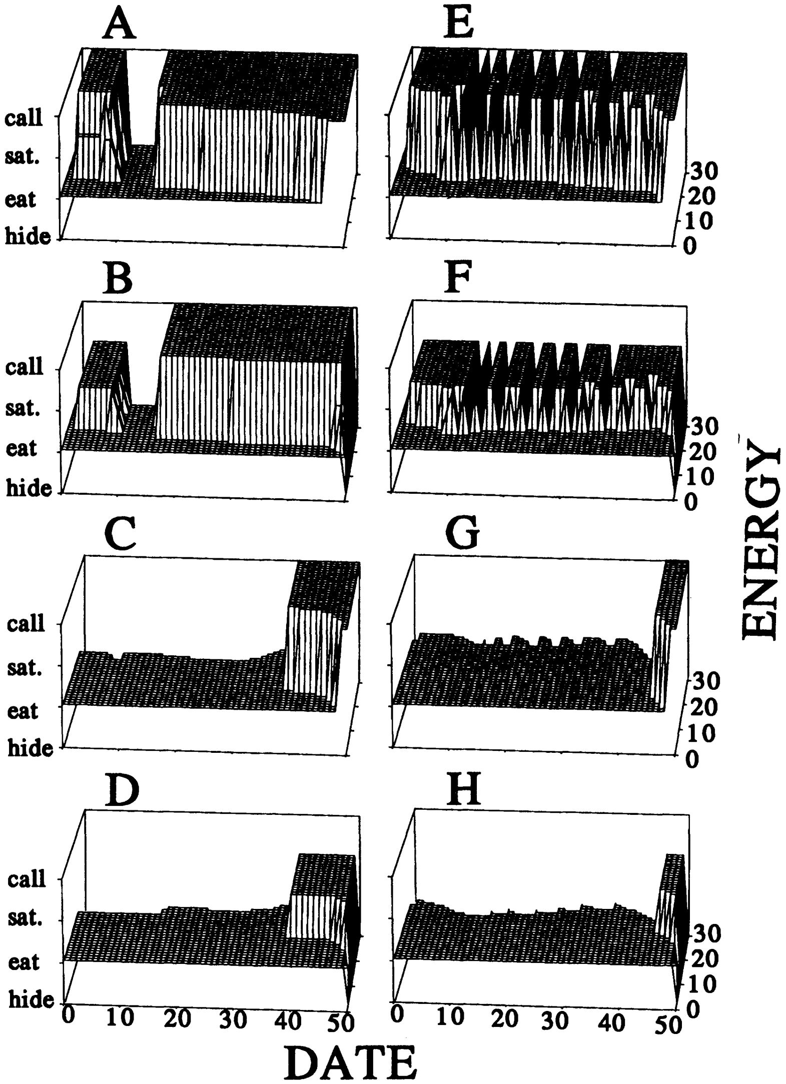

FIG. 3.—Expected male mating decisions as a function of day in the season. and energy state. *A–D* Represent unstable environments ($P_{rain} = 0.2$); *E–H* represent stable environments ($P_{rain} = 0.8$); *A* and *E*, rainy day (rd = 0), second-year male; *B* and *F*, rainy day, first-year male; *C* and *G*, drier day (rd = 1), second-year male; *D* and *H*, drier day, first-year male. See the appendix for a list of parameter values.

mental quality. Under the conditions of our model, second-year males should call when in a chorus rather than be satellites, regardless of environmental conditions (fig. 3*A*, *C*, *E*, and *G*). In contrast, when first-year males attend a chorus, they are predicted to call only on the few days it rains in an unstable environment (fig. 3*B*) and play the more energetically conservative strategy of being satellites the day after a rain (fig. 3*D*) and in stable environments both on the day of a rain

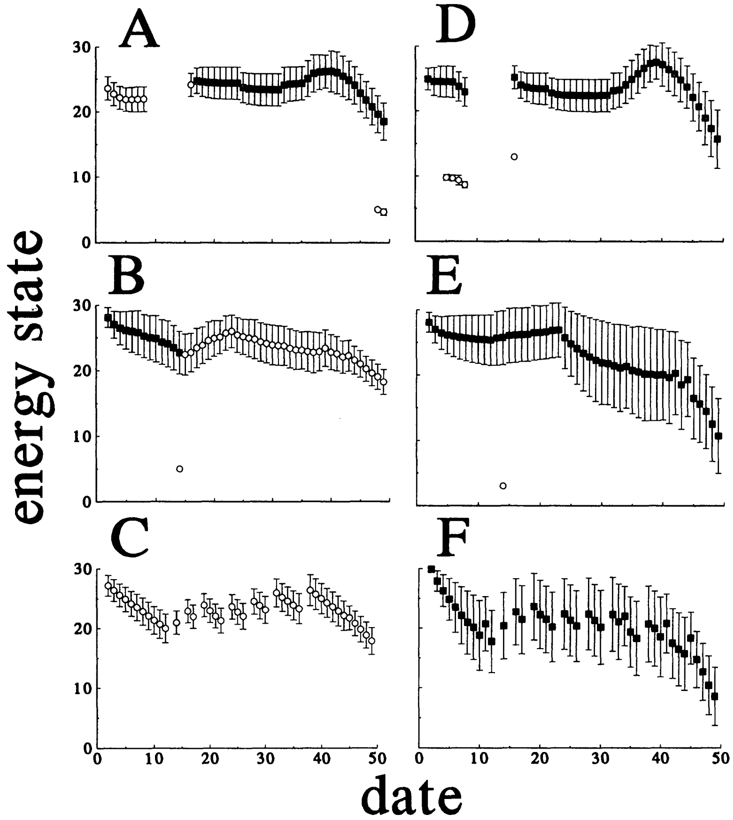

FIG. 4.—Mean ± σ energy stores of males for the basic model in three different types of environments when rd = 0, plotted as a function of day in the season. *A–C*, First-year males; *D–F*, second-year males; *A* and *D*, unstable environment (P_{rain} = 0.2); *B* and *E*, intermediate environment (P_{rain} = 0.4); *C* and *F*, stable environment (P_{rain} = 0.8). Solid squares indicate callers, and open circles indicate satellites. See the appendix for a list of parameter values.

and the day after (fig. 3*F* and *H*). As a consequence of these differences in age-specific mating tactics, second-year males are predicted to show a greater reduction in mean energy stores over the season than are first-year males (fig. 4). That is, old males should choose to adopt riskier mating tactics than young males because their expected future reproductive success is lower than that of young males.

Future Reproductive Success and Density Dependence

Seasonal trends in mating behavior result from a trade-off between two factors. First, because the number of males that can potentially enter the chorus declines seasonally (because of predation and starvation), males should be selected to attend choruses early in the season, when more males are available to form larger choruses (which should decrease the per capita predation risk) and when female arrival rates are closer to their theoretical maxima (because of larger chorus sizes). Second, because the expectation of future reproductive success declines as the season progresses (because of fewer total mating opportunities during that season and a chance of dying before the next season), males should be selected to attend choruses late in the season. Obviously, this effect should be stronger in second-year males than in first-year males because the latter can survive one more year and the former cannot.

The balance between early and late reproduction should be governed by the form of the chorus-size mating payoff function and by the degree of environmental stability. As the season progresses, some first- and second-year males die from predation and starvation, which results in a general decline in chorus size (fig. 5). However, under some conditions, first-year males cease reproductive activities altogether. If female arrival rate is an accelerating function of chorus size (e.g., $\gamma_{\xi 2} = 1$), first-year males should be more likely to drop out of a chorus in the latter part of the breeding season (fig. 5*B* and *C*), because with an accelerating function, mating success drops sharply as chorus size declines. At some point, the population will drop below the minimum number required for first-year males to remain in the chorus. If female arrival rate is a decelerating function of chorus size (e.g., $\gamma_{\xi 2} = -1$), mating success is less sensitive to changes in chorus size, so first-year males should remain in the chorus through the end of the season (fig. 5*E* and *F*).

These predictions hold only for relatively stable environments. If rainy days are infrequent, males should not pass up any mating opportunities during the season. Thus, in unstable environments, first-year males should remain in the chorus through the end of the breeding season, irrespective of the shape of the female arrival function (fig. 5*A* and *D*). First-year males should also tend to call on rainy days in unstable environments (fig. 5*A* and *D*), because they will have adequate time to recoup energetic losses on drier days.

Additional trends predicted include an absence of early chorus attendance by males in both age classes in unstable environments (fig. 5*A*) and differing seasonal patterns of mating tactics employed by first- and second-year males (fig. 5*B*–*F*) in the three types of environments. The latter trend provides insights useful in interpreting the former. Regardless of the degree of environmental stability and the form of the female arrival function, second-year males are always predicted to call when in choruses. In the most stable environment, first-year males are almost always predicted to adopt satellite tactics when in choruses (fig. 5*C* and *F*). In intermediate environments, first-year males should call when in choruses during the early part of the season and then switch to satellite tactics for the remaining part of the season, regardless of the shape of female arrival function (fig. 5*B* and *E*). In unstable environments, first-year males should always call when in choruses if the female arrival function is accelerating (fig. 5*A*). If the female arrival function is decelerating, first-year males should adopt satellite tactics early in the season and call later (fig. 5*D*). Such increased calling activities in unstable environments result from an overall reduction, relative to those of stable environments, in expected daily energy expenditures and mortality risks. In unstable environments, rainy days rarely occur, and choruses rarely form; as a result, males forage more and suffer lower risks of predation. When it does

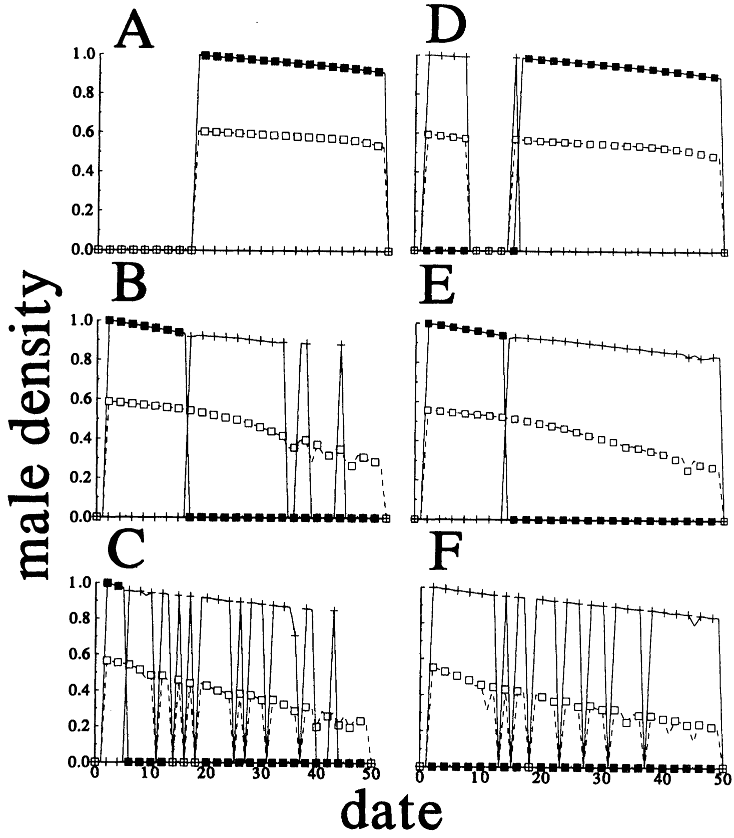

FIG. 5.—Density of callers and satellites in each age-group for two different models in three different environments when rd = 0. Here, *male density* is the fraction of first-year males available at the beginning of the season that survive to day *date* and either call or act as satellites. *A–C,* Accelerating female arrival rate as a function of chorus size ($\gamma_{\xi 2} = 1$); *D–F,* decelerating female arrival rate as a function of chorus size ($\gamma_{\xi 2} = -1$); *A* and *D,* unstable environment ($P_{rain} = 0.2$); *B* and *E,* intermediate environment ($P_{rain} = 0.4$); *C* and *F,* stable environment ($P_{rain} = 0.8$). Other parameter values are listed in the appendix. Solid squares indicate calling first-year males, open squares indicate calling second-year males, and plus signs indicate satellite first-year males. The density of second-year satellites is never > 0.01.

rain, the relatively low male mortality rate (because of high chorus size) and high energy state of most males ensure a large number of calling males of both age classes in choruses.

The absence of an early chorus in unstable environments with accelerating female arrival rates (fig. 5*A*) is predicted to result from a conflict between first- and second-year males in the optimal mating tactic. The mating success of second-year males would be highest early in the season if the chorus size were maximal, that is, if all first- and second-year males called. However, the mating success of first-year males would be highest if they were to adopt satellite tactics and only second-year males called. This would significantly reduce the mating success of calling second-year males, because smaller choruses should attract fewer females, and the females attracted would be shared with satellite males. The only stable resolution to this conflict is for neither age class to join choruses early in the year and for all males to call late in the year.

This conflict between first- and second-year males should be less severe if the female arrival function is decelerating: as chorus size is reduced, more females should arrive than would be the case if the female arrival function were accelerating. As a result, a brief chorus is predicted early in the season, in which second-year males call and first-year males are satellites (fig. 5*D*).

The importance of satellites in this conflict can be illustrated by reducing the mating success of satellites in the model (to $\gamma_{sat} = 0.2$). Under this condition, the chorus should last the entire season, and both age classes should call all season, irrespective of the shape of the female arrival function. These results show that the threat of parasitism by satellites can affect seasonal patterns in mating behavior, even when neither age class exhibits satellite behavior (as in fig. 5*A*).

Gradual Maturation of First-Year Males

Thus far, we have assumed that first-year males could reproduce on the first day of the season. If we assume instead that the proportion of first-year males attaining sexual maturation increases gradually during the season, then a number of predictions are altered. For example, the length of the season should be contracted (at least when $P_{rain} = 0.4$ or 0.8; cf. fig. 5*E* and *F* with fig. 6*B* and *C*), and early maturing first-year males should be satellites early in the season and call later, regardless of environmental stability (fig. 6*A*–*C*).

The predicted switch from satellite to caller could result from density-dependent payoffs: as they increase in number, it may become more advantageous for young males to call if they are joined by a large number of same-aged males. Density-dependent payoffs could also generate the predicted reduction in season length: low payoffs at low chorus sizes could make chorus attendance unstable for both age classes. However, the two sources of density dependence in the model (predation risk and female arrival rates) surprisingly have very different effects on the results. This can be illustrated by holding each factor constant (i.e., independent of male density).

Density-dependent predation risk has little effect on the predictions: the predictions are similar for density-dependent predation risk (fig. 6*A*–*C*) and a constant predation risk of 3.5% per night for calling males (the predation level on second-year males early in the season in the simulation with density-dependent predation; fig. 6*D*–*F*). If predation rate is lowered to 1.5% per night (the level experienced late in the season in the simulation with density-dependent predation), first-year males are predicted to call more, and the chorus is predicted to last longer than when predation rates are higher (fig. 6*G*–*I*). Thus, the mean level of predation should affect the degree to which young males call in the chorus (instead of parasitizing callers), but density dependence, per se, is unimportant.

Eliminating density dependence in female arrival rates qualitatively alters the predicted population dynamics. The breeding season is predicted to be longer in

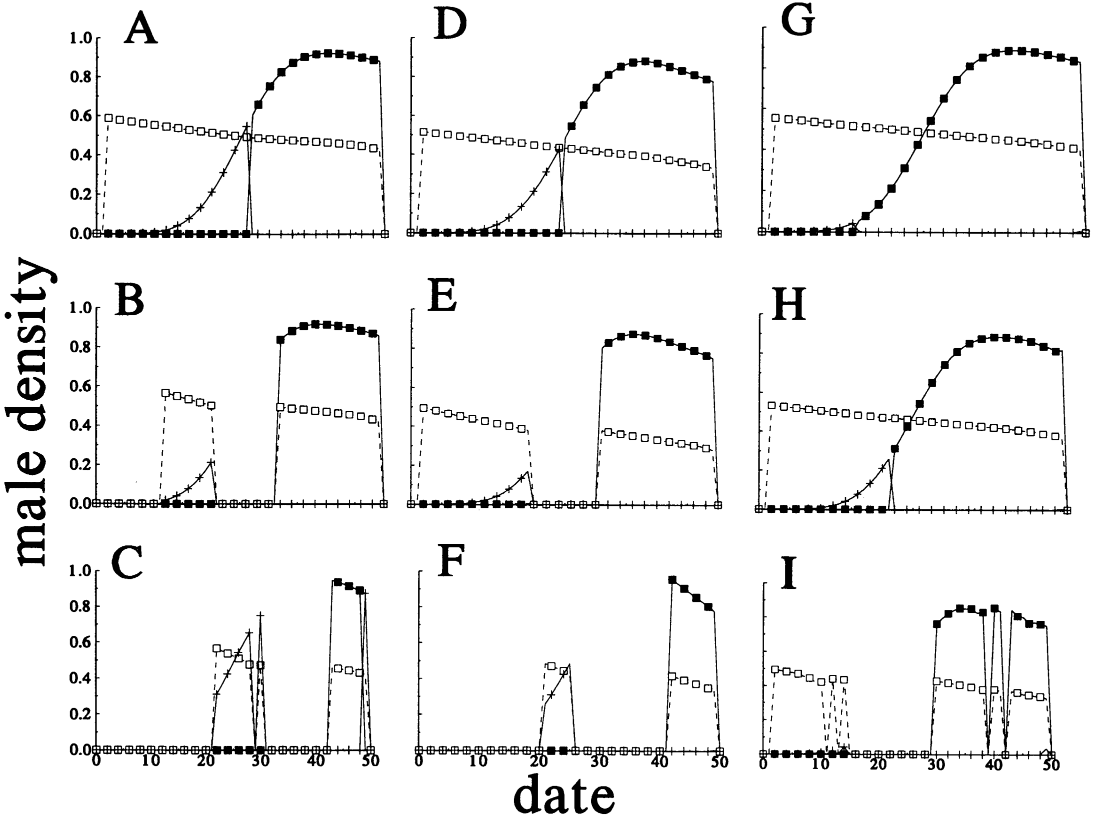

FIG. 6.—Density of callers and satellites in each age-group for three different models in three environments when rd = 0. All models assume gradual arrival of first-year males into the population (see fig. 1). *A–C*, Predation risk decreases with increasing chorus size (see eqq. [3] and [4]); *D–F*, predation risk is constant (3.5% per day for callers in the chorus); *G–I*, predation risk is constant (1.5% per day for callers in the chorus). For *A*, *D*, and *G*, $P_{rain} = 0.2$; for *B*, *E*, and *H*, $P_{rain} = 0.4$; for *C*, *F*, and *I*, $P_{rain} = 0.8$. See fig. 5 for details.

more stable environments, and first-year males should rarely call (cf. fig. 6*B* and *C* with fig. 7*B* and *C*). On drier days, males should also be more likely to enter choruses than when female arrival rates are density-dependent (cf. fig. 7*D–F* with *G–I*).

Finally, density-independent female arrival rates could result in unstable mating systems, particularly in stable environments ($P_{rain} = 0.8$) where no ESS exits (or at least the algorithm finds none). By definition, the system of male mating tactics is stable when the best a mutant male can do is to exhibit the same behavior used by everyone else in the population. This condition never holds with density-independent female arrival rates in stable environments, because mutant callers would have very high mating success in a population of foragers and would quickly invade the population. However, a large population of callers will, in turn, be invaded by satellites. Finally, a mutant forager will be able to invade a population with a large number of satellites. One result of these relationships could be a change in the frequency of male mating tactics in the population. However, with density-dependent female arrival rates, this cycle is broken: a mutant caller in a population of foragers will not attract many females, so a population of foragers will tend to be stable. The instability also results from a tendency for the population to cycle between chorusing and foraging in stable environments, even when conditions permit evolutionary stability (i.e., with density-dependent female arrival rates; see fig. 3*E* and *F*). In unstable environments in which rainy days are less common, foraging on rainy days is less common, and there is no underlying tendency for the population to cycle between foraging and chorusing; as a result, the system is stable, even with density-independent female arrival rates.

Competitive Relationships between Age Classes

In all of the models discussed above, we assume that young males can only attract 70% of the females that old males attract and that this old male mating advantage is independent of the densities of the two age classes. However, females might preferentially choose old males, or young males may be less capable of defending territories than are old males, when the number of old males in the chorus is high. In either case, the mating success of young males would decrease as the number of old males increased.

While the existence of competitive relationships between age classes has been often suggested (see, e.g., Howard 1984; Howard and Kluge 1985; Krupa 1989), no quantitative descriptions of such competition have been published to date. Therefore, we have arbitrarily chosen to represent the mating success of young males as a decelerating function of the number of old callers ($\beta_\Gamma = 0.5$; fig. 2*B*) and to compare predictions of this model with those of the basic model, in which first-year male mating success was fixed at 0.7. For simulations with the decelerating mating success function, the equilibrium densities of old males cause the mating success of young males to be roughly 70% of that of old males; thus, a comparison of a fixed mating success and the decelerating mating function should indicate how the shape of the curve affects predicted mating behavior. Specifically, for the parameter values used in our model, the relative mating success of

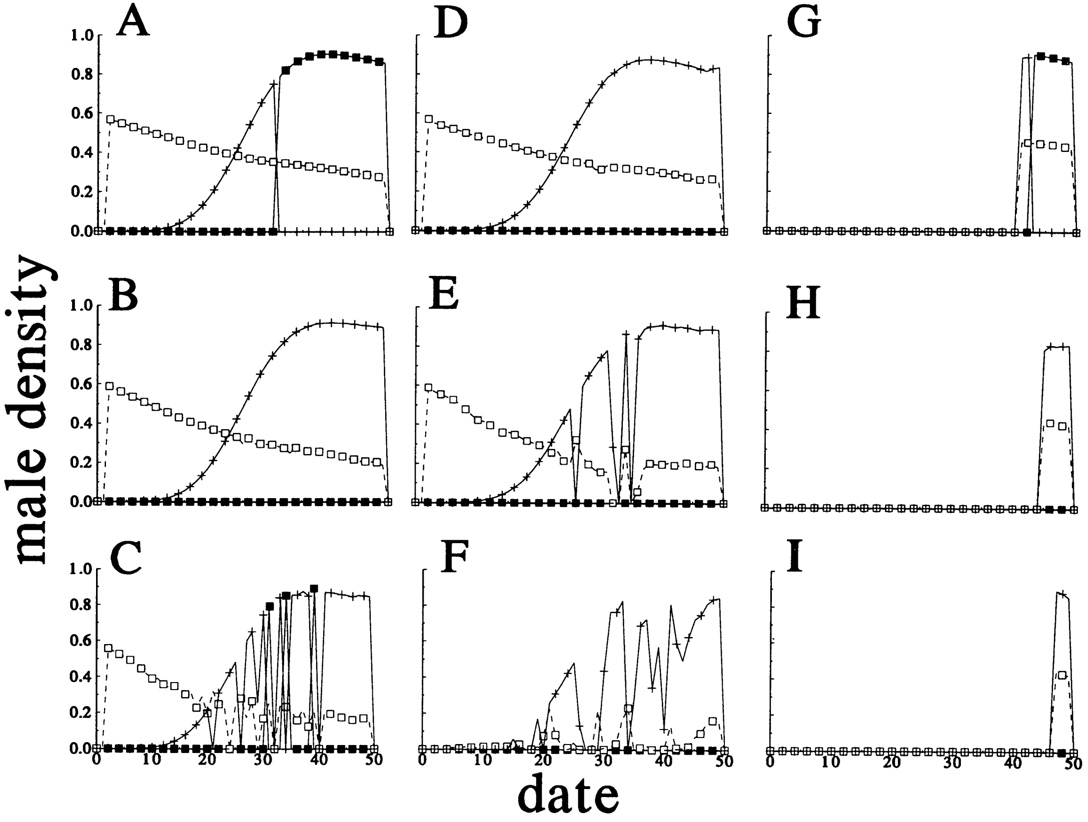

FIG. 7.—Density of callers and satellites in each age-group for three different models in three different environments. All models assume gradual arrival of first-year males. *A–C*, Male densities when rd = 0, female arrival rate is independent of male density (ξ[date, rd] = 0.25); *D–F*, male densities on drier days (rd = 1), female arrival rate is independent of male density (ξ[date, rd] = 0.25); *G–I*, male densities on drier days (rd = 1), female arrival rate increases in a decelerating fashion with chorus size (see eq. [7]; parameter values as in fig. 6*D–F*). For *A*, *D*, and *G*, P_{rain} = 0.2; for *B*, *E*, and *H*, P_{rain} = 0.4; for *C*, *F*, and *I*, P_{rain} = 0.8. See fig. 5 for details.

first-year males ranges from 0.5 to 0.63 for a simulation in which $P_{rain} = 0.2$, from 0.58 to 0.74 for $P_{rain} = 0.4$, and from 0.52 to 0.65 for $P_{rain} = 0.8$. The comparison shows that the shape of the mating success function can qualitatively alter predictions. Compared with a fixed mating success, the mating success of first-year males is, on the average, slightly lower with the decelerating function, yet the ESS solution is for them to call more (compare fig. 5*D–F* with fig. 8*A–C*). The behavior of the second-year males is also predicted to change: the season is longer in unstable environments (fig. 8*A*) but shorter in stable environments (fig. 8*B* and *C*).

DISCUSSION

A major goal of our simulations is to assist field researchers in prioritizing data collection by indicating the type and level of precision of data needed on mating behavior. For example, our models indicate that to explain male mating tactics, we need to quantify the exact relationships between female arrival rate (per calling male) and both chorus size and environmental quality. In contrast, rough estimates of predation risk will suffice; it is not necessary to specify how predation risk varies with chorus size. This information is of considerable practical significance, because predation rates are notoriously difficult to measure (Lima and Dill 1990); however, data on female arrival rates and chorus size should be relatively easy to obtain.

Unfortunately, published data on female arrival rates are sometimes not sufficient enough to be useful. For example, several authors have reported a positive correlation between the total number of females arriving in choruses and chorus size (e.g., Woodward 1984; Gerhardt et al. 1987; Hoglund and Robertson 1987; Odendall and Iwasa 1987). These data are insufficient for this model because female arrival rates must be expressed relative to the number of calling males (fig. 2), and chorus sizes must be defined in terms of the number of calling males rather than all the males in a breeding aggregation. These refinements are necessary because a positive correlation between total female arrival rate and chorus size (even when defined just in terms of calling males) could occur when the correlation between female arrival rate per calling male and chorus size is either positive or negative. Data on female arrival rates do exist for some anuran species and reveal an intriguing diversity of patterns: in some species, female arrival rate increases with chorus size (see, e.g., Wagner and Sullivan 1992; Tejedo 1993); however, the exact form of the relationship (i.e., linear, accelerating, or decelerating) is unclear from this published information. A linear increase is indicated in one study (Ryan et al. 1981). In some species, female arrival rate actually decreases with chorus size (see, e.g., Sullivan 1986); in others, no pattern can be discerned (see, e.g., Arak, 1988*b;* Krupa 1989; Telford and van Sickle 1989; Dyson et al. 1992). Unfortunately, few data exist on female arrival rates in species other than anurans. In the desert grasshopper (*Ligurotettix coquilletti*), a species with both calling and satellite males, female arrival rate per calling male increases with male density (Greenfield and Shelly 1985).

The relative shape of the female arrival rate function and level of environmental stability are predicted to affect the temporal pattern of male mating behavior.

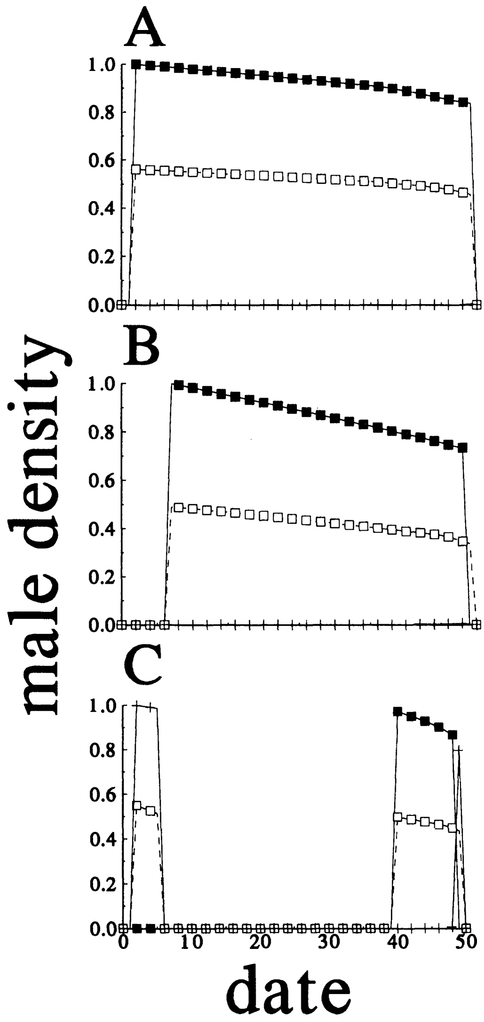

FIG. 8.—Density of callers and satellites in each age-group when rd = 0 and the mating success of young males is dependent on the density of old males in three different environments ($\beta_\Gamma = 0.5$, see eq. [16]; other parameter values are listed in the appendix). All models assume that all first-year males can enter the chorus on the first day of the breeding season. *A*, Unstable environment ($P_{rain} = 0.2$); *B*, intermediate environment ($P_{rain} = 0.4$); *C*, stable environment ($P_{rain} = 0.8$). Solid squares indicate calling first-year males, open squares indicate calling second-year males, and plus signs indicate satellite first-year males. The density of second-year satellites is never > 0.01.

With an accelerating female arrival function ($\gamma_{\xi 2} > 0$) in fairly stable habitats ($P_{rain} \approx 0.8$), first-year males should abandon the chorus before old males. This is based on the assumption that first-year males have lower reproductive success than old males (and therefore future reproductive success is fairly high for this age class), and current reproductive success decreases at the end of the breeding season, in part because of time constraints and in part because of a reduction in male density. In less stable habitats (e.g., $P_{rain} \approx 0.2$; e.g., where female arrival depends on periodic rains), young males should remain in choruses as long as old males. A reduction in environmental stability reduces the relative cost of joining a chorus on high-quality days, because there are fewer high-quality days. Similarly, young males in less stable habitats have relatively more to lose when they leave the chorus on high-quality days. These mating patterns should not occur when female arrival rates decelerate with chorus size or are independent of chorus size, and they illustrate the decreased chances of mating success for males that join small choruses when accelerating female arrival functions pertain. Unfortunately, we know of no data sets that are sufficiently detailed to test these predictions. However, given the documented variation among species in female arrival rates discussed above,. such tests are feasible.

Seasonal variation in the mating tactics used by first-year males are also predicted under some conditions. If female arrival rate accelerates with chorus size and all first-year males are reproductively competent at the beginning of the season, the frequency of satellite behavior is predicted to remain constant or increase during the season in relatively stable habitats ($P_{rain} = 0.8$; Lucas et al., in press). We know of no species in which the increasing pattern has been described, although Roble (1985) described a bimodal pattern (high both early and late in the season) in satellite frequency in *Hyla picta*. In contrast, in species that occupy less stable habitats ($P_{rain} = 0.2$) and have decelerating female arrival rates, or in species in which young males vary when they attain sexual maturity during the season, first-year males should be satellites early in the season and then switch to calling later. The latter situation has been documented in *Hyla cinerea* (Garton and Brandon 1975) and *Rana catesbeiana* (Howard 1984).

The degree to which individuals employ satellite tactics at any point in the breeding season is predicted to vary both between and within age classes. Underlying causes for this variation include residual reproductive value, relative attractiveness to females, energy state, relative costs of alternative tactics, and availability of females. Variation between age classes should largely result from age-specific differences in residual reproductive value and relative attractiveness to females when calling. Variation within an age class should be more affected by energetic state and the relative energy cost of alternative tactics. Given the energy and predation costs assumed in the models above, old males use a fixed mating strategy when in choruses: they always call regardless of variation in female arrival rate and environmental stability. This occurs because they are at peak attractiveness to females and because their residual reproductive success is small (and indeed declines to zero at the end of the breeding season) relative to the current mating success gained by calling. Higher predation risk and higher energetic cost of calling would select for some satellite behavior in second-year males (Lucas et al., in press).

For first-year males, residual reproductive value remains high throughout the season, and they have yet to reach their maximum degree of attractiveness. As a result, they may use either a fixed strategy (e.g., always be a satellite) or a mixed strategy, in which they switch mating tactics during the season. In stable environments, energetic costs are compounded because most days favor the formation of the chorus; under these conditions, first-year males should be satellites. In unstable environments, favorable days are less common, so first-year males can afford to expend additional energy as callers (see also Lucas et al., in press).

Tests of the model predictions are hampered somewhat by lack of data on the ages of callers and satellites for most species. In some species, satellites are significantly smaller than callers (see, e.g., Howard 1984; Forester and Lykens 1986; Arak 1988*a;* Given 1988*b;* Krupa 1989; Backwell and Passmore 1991; Haddad 1991); however, in other species, satellites and callers are similar in size (see, e.g., Roble 1985; Perrill and Magier 1988; Sullivan 1989). Assuming that satellites are younger than callers in the former species and not in the latter, we predict that factors such as age-specific differences in residual reproductive value or in attractiveness to females are critical in the former species and that differences in energy state are important in the latter. That is, callers should have higher energy levels than satellites when age does not influence mating tactics. Similarly, even in systems in which most satellites are young males, if any old males act as satellites, we predict that they will have lower energy reserves than old calling males. In *Uperolei rugosa,* for example, satellites are either young males or old males that have lost weight as a result of prior calling and territory defense (Robertson 1986). Studies on *Eleutherodactylus johnstonei* (Ovaska and Hunte 1992) and *Bufo cognatus* (Krupa 1989) provide additional support for this prediction.

We have assumed that competition for mates among males of different ages can take one of two forms: either first-year males attract some fixed proportion of the females that a second-year male attracts, or the frequency of old males determines the mating success of young males. Correlations between age and male mating tactics have been observed in several taxa other than anurans, including fish (Kodric-Brown 1977), crickets (Greenfield and Shelly 1985), deer (Clutton-Brock et al. 1979), and elephant seals (LeBoeuf 1974). In each of these cases, age differences in mating tactics correlate with age differences in the ability to compete against other males for mates. However, the form of this competition is less clear. Density-dependent competition has been implicated in several studies (Howard 1978; Wells 1978; Robertson 1986; Given 1988*b*). There is also some evidence that calling males that lose fights become satellites on the winner's territory (see, e.g., Given 1988*b;* Wagner 1989); these interactions could also influence the density-dependent payoffs to chorus attendance. The distinction is important because it potentially alters the predictions of the model: first-year males in systems in which mating success is affected by the density of old males should be more likely to become satellites than first-year males in systems in which mating success is a fixed fraction of the mating success of second-year males.

Our models predict that, in fairly stable environments, the chorus might not form on suitable rainy nights, which creates periods of chorusing punctuated by a day or more of reproductive inactivity (see Lucas et al., in press). The basis of the prediction is an interaction between the energetic cost of calling and several positive feedback mechanisms. When environmental conditions promote female arrival on most days of the season, males cannot remain in the chorus every day if the energetic cost of attendance is high. Such limited chorus attendance by individual males is quite common in anurans (Murphy 1992). The average number of consecutive days that a male resides in a chorus varies from 3.3 d in *Hyperolius marmoratus* (Dyson et al. 1992) to 18.3 d in *Hyla rosenbergi* (Kluge 1981). An average residency duration of about 7 d has been reported for several species (see, e.g., Wells 1977*b;* Fellers 1979; Godwin and Roble 1983). In addition, calling males have been shown to experience daily or seasonal weight loss in a number of species (Wells 1978; MacNally 1981; Arak 1983; Robertson 1986; Given 1988*b;* Cherry 1993). Under the assumptions of our model, fitness is enhanced at high chorus sizes because of a density-dependent increase in female arrival rate and a density-dependent reduction in predation risk. These density-dependent mechanisms select for increased synchronization of the chorus; as some males are forced to leave the chorus because of energetic demands, the resultant small chorus provides reduced fitness opportunities for other males, causing them to forgo chorusing. Wave patterns are not predicted in unstable environments because when rainy days are uncommon, all males should attend the chorus on those few days when environmental conditions promote high female arrival rates. Chorus sizes during the breeding season are highly variable in some species of prolonged breeders (see, e.g., Fellers 1979; Kluge 1981; Godwin and Roble 1983; R. D. Howard, unpublished data). Although some of this variability is due to unsuitable weather, our models suggest that wave patterns should also result from intrinsic factors that are independent of environmental conditions. In addition, while the predictions do not necessarily assume that males can judge chorus size, there is some evidence that male frogs can indeed perceive chorus size and regulate their mating behavior accordingly (Jennions and Backwell 1992).

The results from our models generally reflect trade-offs between future and immediate reproductive success inherent in behaviors available to each male. For example, males with low energy states are predicted to forage instead of entering a chorus, and the threshold energy state above which males should enter a chorus is predicted to decline toward the end of the season (at least for old males). As the season progresses, second-year males should be more willing to enter a chorus, because this is their only means of realizing a reproductive payoff. However, conflicts between individuals in the choice of mating tactics may result in mating patterns that are not optimal for any male. For example, choruses are not predicted to form early in the season in unstable environments when female arrival rate accelerates with increasing chorus size. Under these conditions, males of both age classes realize higher reproductive payoffs if they both enter a chorus, but old males only benefit if young males call at this time, whereas if old males call, young males benefit more by becoming satellites. The only stable solution is for neither age class to enter the chorus, despite both age classes having higher fitness if all males called. This scenario underscores the potential for satellite pressure to influence the dynamics of anuran choruses, even when there are no satellites in the population.

Several previous models have dealt with the evolution of alternative mating tactics. These models generally deal with factors that we do not address here and are therefore complementary to our model. For example, Waltz (1982) proposes a graphic model to explain why males choose to become satellites, when reproductive success of satellites is typically lower than that of callers. The model is based on the polygyny threshold model (Orians 1969) and assumes that males settle sequentially onto territories of unequal quality. Later-arriving males would have only lower-quality territories available to them and so might do better if they were satellites in higher-quality territories instead of calling from lower-quality territories. Waltz (1982) assumes that callers in high-quality territories attract more females than they could mate with; these excess females constitute the quality of that territory for a satellite. If satellites take only excess females, the frequency of satellites in the population will not affect the payoff to callers. This would invalidate the assumption in our model that caller mating success is a function of the frequency of satellites in the population. Female arrival rates in some species may be so high that resident males cannot mate with all females they attract; however, direct competition for a limited number of females is common in many species (Wells 1977*a;* Howard 1978; Perrill et al. 1978).

Arak (1988*a*) modeled caller and satellite behavior as a frequency-dependent game. In the model, the attractiveness of a calling male depends on his call intensity relative to that of his neighbors, and satellites compete directly with callers for females drawn into the territory (as we assume in our model). On the basis of a comparison between the predictions of several models and data collected on *Bufo calamita,* Arak (1988*a*) concludes that callers are unlikely to detect the presence of satellites and therefore cannot use this information in the choice of calling site. Arak also shows that males with low-intensity calls tend to be satellites and choose to parasitize males with unusually high-intensity calls, as predicted by his model. This model addresses mating decisions on a finer spatial scale than the one we used; we evaluate the performance of males relative to the entire population, whereas Arak (1988*a*) considers performance relative to a toad's nearest neighbors. Data from *B. calamita* indicate that some of the variation in mating behavior among males can be attributed to local variation in the quality of neighboring males. With respect to our model, the qualitative predictions of the model are not likely to be affected by the spatial scale of competition between males, although the quantitative predictions will almost certainly be affected. Unfortunately, we know of no data that address the relative importance of scale on the evolution of male mating decisions, so at this point, the validity of this assumption is untestable.

Rubenstein (1980) modeled alternative mating tactics for which he assumed that the fitness consequences of satellite behavior are identical to those of callers. While there is some evidence that mating success is similar for callers and satellites (see, e.g., Perrill et al. 1978), satellites generally realize a lower mating success than callers (Waltz 1982). Rubenstein (1980) also assumes that caller and satellite behaviors have evolved as a mixed strategy in which individuals either always choose one of the strategies or choose randomly among the strategies at the frequency that equalizes fitness. Here again, satellite and caller decisions are more generally conditional strategies (as we have modeled them), in which individuals base their decisions on their unique phenotype and in which the fitness of the two strategies is not necessarily equivalent (Greenfield and Shelly 1985; Arak 1988*a*).

All of these previous models have ignored energetic state as a factor in caller and satellite decisions, despite the fact that callers (or, more generally, advertising males) typically expend more energy than satellites (see, e.g., Rubenstein 1980). Arak (1988*a*) treats energetic costs as an alternative to the assumption that decisions are conditioned on relative call intensity and rejects this hypothesis in favor of the conditional strategy hypothesis for *B. calamita*. However, energetic costs and conditional strategies are not mutually exclusive alternatives.

For simplicity, we assumed that calling involves a constant energetic cost for all males. However, data on several anuran species indicate that females are differentially attracted to calls broadcast at higher rates and/or for longer durations (see Gerhardt 1994); males with these call attributes may pay higher energetic costs to increase their attractiveness. One advantage of dynamic game theory is that it provides a theoretical framework to consider the role of both energetic state and other individual conditions or decisions (such as age, call rate, call intensity, and call duration). However, in the case of male calling effort, we need more data on the range of alternative calling rates and call intensities available to males and on the relative costs and benefits of these alternatives. When these data are available, our model could easily be altered to incorporate these additional features of male mating decisions.

None of the previous models of alternative mating tactics incorporate future reproductive payoffs, seasonal effects, male age, or the payoff to males not attending a chorus, despite the fact that all of these factors can play a major role in the dynamics of mating behavior in many species. Of course, models become quite complicated when these factors are added; this is particularly true of standard analytical ESS models (sensu Maynard Smith 1982). Nonetheless, it is important to consider their combined effects, since they give us a more realistic understanding of the evolution of male mating behavior.

We treat male mating decisions as the choice between calling and being a satellite. This dichotomy is found in many anurans, although a third alternative, searching for mates, is exhibited, particularly in explosive breeders (see, e.g., Wells 1977*a;* Arak 1988*a;* Woolbright et al. 1990; Tejedo 1992). While searching males are generally quiet, the dynamics associated with searching behavior are likely to be quite different than those of (stationary) satellite behavior. Thus, conclusions we draw for caller and satellite decisions may not hold for species that are characterized by caller and searcher decisions. Some preliminary models of species with callers and searchers exist (see, e.g., Fairchild 1984; Woolbright et al. 1990); however, no dynamic games have been developed for these alternative tactics. Such an approach seems warranted.

Clark (1993) suggests that dynamic optimization is a unique tool that allows us to bridge the fields of behavioral ecology and life-history theory. Indeed, our models explicitly consider survival and reproductive consequences of alternative behaviors and incorporate trade-offs between current and future reproductive success; these ideas are the basis of life-history theory (Stearns 1992; Clark 1993). In this respect, dynamic game theory provides a tool that enables us to take a truly synoptic view of the evolution of alternative mating behavior.

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APPENDIX

Parameter Values Used for the Basic Model

$a_e = 5.0$, $b_e = 0.10$	Arguments for incomplete beta function relating starvation risk to relative energy state *e*
$a_B = 0.25$, $b_B = 0.10$	Arguments for incomplete beta function relating fraction of first-year males that are reproductively competent to day in season
$a_\sigma = 10.0$, $b_\sigma = 0.35$	Arguments for incomplete beta function relating female arrival rate to day in season
$a_{ow} = 5.0$, $b_{ow} = 1.0$	Arguments for incomplete beta function relating overwinter mortality risk to energy state *e* at the end of the breeding season
$P_c = 0.99$	Probability that the season lasts at least 1 d past the present day
$\gamma_{ow} = 0.75$	Maximum overwinter survival rate
$\beta_1 = 1.33$	Number of first-year males displaced by each calling second-year male
$\beta_\Gamma = 0.5$	Coefficient determining shape of function of relative ability of first-year calling males to attract females as a function of density of second-year males
$\beta_p = 0.05$	Maximum probability that a predation event will occur in a territory in one night during the breeding season
$\beta_{sat} = 0.20$	Satellite mortality rate divided by caller mortality rate
$\mu_{forage} = 0.001$	Probability that a forager is killed in 1 d
$\mu_{hide} = 0.0001$	Probability that a male hiding in a refuge is killed in 1 d
$T_{max} = 50$	Maximum length of the breeding season
$\gamma_{\xi 1} = 0.4$	Maximum female arrival rate (number of females per calling male per night)
$\gamma_{\xi 2} = -1$	Coefficient determining the shape of the relationship between female arrival rate and chorus size
$\gamma_1 = 0.7$	Ability of first-year male to attract a female relative to that of an old male
$\gamma_{sat} = 0.4$	Ability of a satellite to obtain a female relative to that of an average caller
$\Delta\epsilon_{call}\sigma_{\Delta\epsilon} = -2.5 \pm 1.4$	Change in energy state ϵ for 1 d as a result of calling
$\Delta\epsilon_{sat}\sigma_{\Delta\epsilon} = -1.0 \pm 0.6$	Change in energy state ϵ for 1 d as a result of being a satellite
$\Delta\epsilon_{hide}\sigma_{\Delta\epsilon} = -1.0 \pm 0.6$	Change in energy state ϵ for 1 d as a result of hiding in a refuge
$\Delta\epsilon_{forage} \pm \sigma_{\Delta\epsilon} = 4 \pm 1.4$	Change in energy state ϵ for 1 d as a result of foraging

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