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Callers and satellites: chorus behaviour in anurans as a stochastic dynamic game

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Abstract. Males often compete for mates using alternative tactics whose relative success could be simultaneously influenced by four factors: subsequent behaviour, physiological state, the frequency of expression of alternative tactics and the density of competing males. Here the payoffs to two alternative male mating tactics (call and satellite) were examined in anurans using a stochastic dynamic game. The basic model considers an iteroparous species with a prolonged breeding season and fairly low energetic costs and predation risks. The model assumes that female chorus attendance is affected by weather, time of year and male chorusing intensity. Results show that interactions between energetic costs of calling, density-dependent predation risk and female arrival rates, and frequency-dependent mating success produce distinct temporal waves of male chorusing despite continuously favourable environmental conditions. Relative to second-year males, first-year males attended choruses less often and were more likely to become satellites. When the energetic costs of calling were increased, waves became shorter and less frequent, and some older calling males switched to satellite behaviour. Satellites were less common when breeding season length was constrained by extrinsic factors such as seasonal weather patterns. Extrinsic constraints may also affect system stability: if female arrival rates are independent of male chorusing intensity, an evolutionarily stable strategy occurs only if the breeding season is short. Even without extrinsic constraints, the breeding season may be short if predation rates on adults are sufficiently high, or if satellites intercept a large fraction of incoming females. Thus, the ‘explosive’ breeding systems observed in many anuran species could result from either biotic or abiotic causes.

A decision can be thought of as a commitment of time to some particular course of action when an animal has more than one alternative behaviour available to it (Lucas 1985). The choice of behaviour should depend on the relative fitness payoffs accrued from the expression of each of the alternatives (Stephens & Krebs 1986). These payoffs often have four properties. (1) They are sequentially dependent: the immediate payoff to a given behaviour will depend on the sequence of behaviour patterns an animal is expected to show in the future (e.g. Houston & McNamara 1982; Lucas 1983). (2) They are state dependent: the animal’s physiological state (including fat levels, glycogen levels or hormone levels) may affect the relative advantage of alternative behaviour patterns (e.g. Mangel & Clark 1988; Lucas & Walter 1991). (3) They are frequency-dependent: the fraction of individuals in a population exhibiting each alternative may affect the payoff to expressing any given behaviour (e.g. Maynard Smith 1982; Parker 1984). (4) They are density dependent: in addition to the fraction of individuals exhibiting the behaviour, the absolute number of individuals that show a behaviour may also be important (e.g. Nee & May 1993; Read & Harvey 1993). Any one of these properties complicates the study of behaviour; until recently, the simultaneous evaluation of all four properties has been virtually impossible.

Ignoring any one of these properties may lead to an incomplete understanding of the evolution of behavioural traits. For example, Nee & May (1993) elegantly demonstrated that both

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frequency- and density-dependent selection affect the evolution of intraspecific brood parasitism, although this phenomenon is usually modelled as if the payoffs were only frequency dependent. Houston & McNamara (1988) demonstrated that adding a state variable to the classic hawk-dove game can lead to further insight than that provided by the original, state-independent game. Here we provide a framework for a model of the evolution of behaviour that incorporates all four properties listed above. The model is based on the frequency-dependent stochastic dynamic game of Houston & McNamara (1987, 1988), but incorporates density-dependent payoffs as well.

Here we model alternative mating tactics in anurans. In a variety of vertebrate and invertebrate taxa, some males attract females into territories that they defend from rival males, and other males employ alternative tactics to obtain mates. Alternative tactics include female mimicry, forced copulation, cuckoldry and satellite behaviour (see Dunbar 1982; Arak 1984 for reviews). Satellite behaviour in particular is a common alternative mating tactic in anurans. In general, satellite males associate themselves with males that are actively advertising to attract females and attempt to intercept and mate with females that approach these advertising males. Satellites have also been reported in birds (e.g. ruffs, *Philomachus pugnax*: van Rhijn 1973), mammals (e.g. topi, *Damaliscus lunatus topi*: Gosling & Petri 1990), fish (e.g. bluegill sunfish, *Lepomis macrochirus*: Gross 1982) and invertebrates (e.g. crickets: Rowell & Cade 1993). Satellite behaviour appears to be particularly pervasive in anuran amphibians, however. Satellites have been reported in *Rana clamitans* (Wells 1977a), *R. catesbeiana* (Howard 1978, 1984), *Hyla cinerea* (Garton & Brandon 1975; Perrill et al. 1978), *H. versicolor* (Fellers 1979), *Pseudacris regilla* (Perrill 1984), *P. crucifer* (Forester & Lykens 1986), *Acris crepitans* (Perrill & Magier 1988), *Bufo calamita* (Arak 1988; Tejedo 1992), *B. cognatus* (Krupa 1989) and many other species.

Several models of satellite behaviour in anurans have been published. Waltz (1982), in a general review of satellite behaviour, discussed the 'satellite threshold model', which models satellite frequency as a function of the attractiveness of a 'dominant' male. Arak (1988) addressed a similar problem: whether males should call or become satellites as a function of the size or attractiveness of other males in the vicinity. These models may be inadequate in their ability to predict the frequency of satellites in choruses, however, because they consider only one factor that affects a male's decision to call or play satellite, the relative ability to attract mates. Predation risk, energetic costs, life-history factors and environmental cues will also influence the frequency of satellites in a population.

Satellites may suffer lower immediate reproductive success than callers, but at a lower expense in terms of both predation risk (Jaeger 1976; Howard 1978; Ryan et al. 1981) and energy expenditure. Greater survival prospects, in turn, affect future reproductive success and therefore make behavioural payoffs sequence dependent. Because calling is energetically expensive (e.g. Bucher et al. 1982; Taigen & Wells 1985; Ryser 1989; Grafe et al. 1992; Cherry 1993), the choice of mating tactic is also likely to be state dependent. Arak (1988) discussed an evolutionarily stable strategy (ESS) model of anuran reproductive tactics, explicitly considering the frequency of satellites and callers in the chorus. Finally, several factors influencing male fitness in choruses are density dependent, including predation risk (Ryan et al. 1981; see Lima & Dill 1990, for a general review), and female arrival rates (e.g. Ryan et al. 1981; Dyson et al. 1992; Wagner & Sullivan 1992).

In our analysis, we addressed several issues that relate to evolutionary aspects of calling in anurans: (1) the effect of the presence of satellites on calling decisions and the temporal pattern of the chorus, (2) how the energetic cost of calling (and generally of chorus attendance) affects anuran mating behaviour, (3) the effect of frequency dependence in mating success on the temporal stability of choruses, (4) how weather-related constraints that regulate breeding season length affect mating behaviour, (5) the role of density-dependent predation risk and overall longevity in a male's reproductive tactics, and (6) the effect of the relationship between chorus size and female arrival rate on the chorus.

THE MODEL

Anuran mating behaviour was modelled as a stochastic dynamic game, following the general algorithm suggested by Houston & McNamara (1987, 1988). Our model assumes that the game is an alternative-option scramble (Parker 1984), or, in Maynard Smith's (1982) terms, 'playing the field', where each individual has two or more alternative options and the payoffs to these options depend on direct competition with other individuals in the population. The algorithm has two parts. For the first part, we start with some initial guess about the fraction of males that show each behaviour on each day of the season and then use dynamic programming (e.g. Mangel & Clark 1988) to determine the best sequence of behaviour patterns that a 'mutant' male should play against this population. This essentially finds the best mutant tactic against the initial population. The second part of the algorithm then simulates a population of these best mutants to estimate the fraction of males in this new mutant population that play each tactic on each day of the season. This two-step process, a dynamic programme using backward iteration to determine the optimal sequence of decisions followed by an iteration forward in time simulating a population composed entirely of the mutants, is then repeated until the best reply to the population is the tactic that the population itself is playing. This is the Nash equilibrium. There are conditions where no stable tactic was reached (see below; see also Houston & McNamara 1987), however, and in this case the model was iterated 50 times and the results from the last iteration are reported here.

We assume that male anurans can perform four different behaviour patterns (hide, forage, satellite and call) and seek the sequence of state-dependent rules that males should exhibit during the season such that, if all males in a population exhibit these rules, no mutant individual with some other rule can invade the population. Two of the behaviour patterns represent alternatives available to males not attending a chorus: they can forage or hide in a refuge without foraging. The other two behaviour patterns are only performed while in a chorus: males can call to attract females (and incidentally predators), or become satellites to intercept females attracted to calling males (Wells 1977a, b; Howard 1978; Perrill et al. 1978). Males are assumed to choose between the alternative behaviour patterns once a day, and there is no constraint on the ability to switch their behaviour between days. Switching has been observed in many species (e.g. *R. catesbeiana*: Howard 1984; *H. cinerea*: Gerhardt et al. 1987; *B. calamita*: Arak 1988; *A. crepitans*: Perrill & Magier 1988; *Eleutherodactylus johnstonei*: Ovaska & Hunte 1992), and seems to be a general property of male mating behaviour.

We know of no single species that has been sufficiently well described to allow a full parameterization of the model. In fact, there are only a few species in which even the qualitative relationships between variables that determine calling behaviour are known. Our only alternative, therefore, was to build a composite species that combines traits that have been described from several different species (Table I).

We consider three fitness components in the model: energetic state (which determines starvation risk), risk of death by predation and mating success (number of females mated). To run the dynamic programme the states and time were divided into discrete intervals.

Time was divided into intervals of 1 day and energetic state was divided into a series of 30 intervals. 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). Thereafter the change in state is probabilistic (i.e. the change in energy on any given day is described by a transition matrix) and is determined by the behaviour shown by the males. Calling is assumed to be the most energetically expensive behaviour. In most species of anurans, males rarely attend a chorus every night of the season. Although numerous factors, such as predation, energy availability, female availability and sperm depletion, could limit chorus attendance, energetics has been implicated as a major cause in several species (e.g. *P. crucifer*: Forester & Lykens 1986; *Uperolia rugosa*: Robertson 1986; *B. cognatus*: Krupa 1989; *B. calamita*: Tejedo 1992; Murphy 1994; but see Arak 1988; Green 1990). Based on these results, we set the energetic cost of calling so that a male with a full energy load could call on average either 4, 12 or 60 consecutive nights without replenishing its energy stores; note that each of these values represents a separate population, so we are modelling some populations in which the cost of calling is high and other populations in which the cost of calling is relatively low. This corresponds to a mean change in energy state ($\Delta\varepsilon_{\text{call}}$) of -7.5,

Table I. Parameter values for the basic model

Variable	Value	Definition
$\Delta\varepsilon_{call} \pm \sigma^2_{\Delta\varepsilon}$	-2.5 ± 2.05	Change in energy state for 1 day due to calling
$\Delta\varepsilon_{sat} \pm \sigma^2_{\Delta\varepsilon}$	-1.0 ± 0.3	Change in energy state for 1 day due to being a satellite
$\Delta\varepsilon_{hide} \pm \sigma^2_{\Delta\varepsilon}$	-1.0 ± 0.3	Change in energy state for 1 day due to hiding in a refuge
$\Delta\varepsilon_{forage} \pm \sigma^2_{\Delta\varepsilon}$	4 ± 2.04	Change in energy state for 1 day due to foraging
a, b	5, 0.1	First and second parameters for incomplete beta function relating probability of starvation for 1 day to energy level
a_1, b_1	5, 1	First and second parameters for incomplete beta function relating the probability of starvation outside of the breeding season to energy level at the end of the season
a_2, b_2	10, 0.35	First and second parameters for incomplete beta function relating the fraction of maximum female arrival rate as a function of date
T	50	Maximum length of breeding season
γ_{call}	0.05	Maximum probability of a caller being depredated in 1 day
γ_{sat}	0.20	Relative predation risk to satellites (see description of model)
γ	0.227	Scaling parameter for increase in female arrival rate with chorus size
γ_1	1	Scaling parameter for strength of quadratic term in relationship between female arrival rate and chorus size
ι_{sat}	0.4	Relative ability (compared to callers) of satellites to intercept females arriving at calling sites
P_{rain}	0.8	Probability that the weather on a given day is sufficiently favourable to promote a maximum female arrival rate
P_c	0.99	Probability that breeding season will continue at least an additional day
$\alpha[1]$	0.7	Relative mating ability of first-year males, as a fraction of the mating ability of older males
maxrd	4	Maximum number of days the weather is poor before females stop arriving at chorus completely

−2.5 and −0.5 units per 24-h period, respectively ($\sigma^2_{\Delta\varepsilon}=2.05$ for each). For simulations where callers lost −7.5 or −2.5 energy units per 24-h period, the cost to satellites ($\Delta\varepsilon_{sat}$) was −1 ($\sigma^2_{\Delta\varepsilon}=0.3$); thus a satellite with a full energy load could attend the chorus for 30 consecutive days on average. Alternatively, when callers lost −0.5 energy units per 24-h period, we assumed that satellites could gain 0.5 energy units ($\Delta\varepsilon_{sat}=0.5$, $\sigma^2_{\Delta\varepsilon}=0.3$). A low energetic cost of calling for both callers and satellites could result from individuals foraging during the day, and thereby recovering some of the energetic costs from the previous night (e.g. as in *R. catesbeiana*: Howard 1984). These satellite costs reflect the likelihood that satellites expend less energy than callers (Forester & Lykens 1986; Krupa 1989). In this model, we are explicitly modelling species where satellites are relatively sedentary. Finally, hiding in a refuge results in the same energetic expenditure as being a satellite ($\Delta\varepsilon_{hide}=\Delta\varepsilon_{sat}$), and foraging generates a net increase in energy such that a male with depleted energy stores could replace its stores in 7.5 days, on average ($\Delta\varepsilon_{forage}=4$, $\sigma^2_{\Delta\varepsilon}=2.04$). These changes in energetic state are assumed to be neither frequency nor density dependent.

The probability of starvation (μ_{st}) over any 24-h period during the mating season is assumed to be a function of energetic state and is simulated using an incomplete beta function (throughout, brackets indicate a function of the bracketed variables):

$$\mu_{st}[\varepsilon]=1-I_{\varepsilon}\{a,b\} \qquad (1)$$

where ε is equal to the current energy state as a fraction of the maximal energetic level, and a and b are constants.

The incomplete beta function of some variable ε ($I_{\varepsilon}\{a,b\}$) is a cumulative distribution that ranges from 0 to 1 for $0 \leq \varepsilon \leq 1$. The arguments of the starvation risk function, a and b, were set so that the risk of starvation was high ($\mu_{st}[\varepsilon]>0.16$) for males less than 3% of their maximum potential energy stores, and starvation was certain ($\mu_{st}[\varepsilon]=1.0$) for males with no energy stores. Starvation risk was low ($\mu_{st}[\varepsilon] < 0.05$) for males with greater than 10% of the maximum energy stores. For iteroparous species, we assumed that overwinter mortality rates (μ_{ow}) were in part determined by the energy stores left at the end of the previous mating season

$$1 - \mu_{ow}[e] = (1 - \mu_{min})\ I_e\{a_1,b_1\} \qquad (2)$$

where $\mu_{ow}[e]$ is the energy state-dependent probability of mortality from the end of a mating season to the beginning of the next, μ_{min} is the minimum probability of mortality (probability of dying for a male with maximum energy stores), and $I_e\{a_1,b_1\}$ is the incomplete beta function for relative mass e (e = percentage of maximum energy stores carried by the male at the end of the season).

Predation risk was assumed to be lowest for hiding and relatively low for foraging, and was neither frequency nor density dependent for either behaviour. In contrast, predation risk in the chorus was assumed to be both density dependent (decreasing with increasing chorus size, as illustrated by Ryan et al. 1981 for *Physalaemus pustulosus*) and frequency dependent (satellites intercept some fraction of the predators attracted to callers). Additionally, satellites typically experience lower predation risk than callers (e.g. Howard 1984; Perrill & Magier 1988); we assume that predation risk to satellites is about 10% of that to callers. Thus calling is a high-cost, high-risk tactic, but satellites suffer low risk and expend less energy. Predation risk to a caller is

$$\mu_{call}[date] = \frac{\gamma_{call}(1 - D_{call}[date])}{1 + (\gamma_{sat} \times D_{sat}[date]/D_{call}[date])} \qquad (3)$$

where γ_{call} equals the maximum probability of a caller being killed per 24-h period, $D_{call}[date]$ and $D_{sat}[date]$ equal caller density and satellite density on a given date (both taken as a fraction of the total number of males alive at the beginning of the season), $D_{sat}[date]/D_{call}[date]$ equals the number of satellites per caller, and γ_{sat} equals relative predation risk to satellites (the predation risk to satellites divided by the predation risk to callers). If γ_{sat} is 0.1, then callers are 10 times more likely than satellites to be taken by a predator.

There are two parts to equation (3). The numerator is the rate at which an individual (satellite or caller) is killed on a caller's territory; this decreases linearly with caller density and has a slope of γ_{call}. The denominator accounts for the fact that satellites can intercept some of these predation events; it is essentially the effective number of individuals on the territory that are at risk of predation. The predation risk to satellites is

$$\mu_{sat}[date] = \mu_{call}[date] \times \gamma_{sat} \qquad (4)$$

Three variables determine mating success: age, satellite frequency and female arrival rate. In several species of anurans (e.g. *R. catesbeiana*: Howard 1984; *U. rugosa*: Robertson 1986), small, young males have lower mating success than larger, older individuals. We simulate this relationship by assuming that a first-year male is able to attract some fraction ($0 \leq \alpha[1] \leq 1$) of the females available to an older male ($\alpha[age] = 1.0$ for $age > 1$). Owing to this age dependence, young calling males will attract fewer than the mean number of females arriving per calling male (of any age), and old calling males will attract more than the mean number. If $p_1[date]$ equals the fraction of first-year males calling in the chorus on a given day, the older males will attract the following proportion of the mean number of females per male

$$\phi[date] = \frac{1}{1 - \{p_1[date] \times (1 - \alpha[1])\}} \qquad (5)$$

and the first-year males will attract $\phi[date]\alpha[1]$ proportion of the mean number of females per calling male. Note that

$$p_1[date] \times \phi[date] \times \alpha[1] + \sum_{age > 1} p_{age}[date] \times \phi[date] \times \alpha[age] = 1 \qquad (6)$$

We assume that the maximum number of females that can arrive on any given night is dependent on the time of year ($\sigma[date]$), and increases from the first day of the season through to the middle of the season, and thereafter decreases. We use an incomplete beta function to model this maximum potential arrival rate

$$\sigma[date] = I_d\{a_2,b_2\} \qquad (7)$$

where *date* equals the number of days since the beginning of the mating season. The variable, d, in the incomplete beta function is a function of date and ranges from 0 (on the first and last days of the season) to 1 (in the middle of the season). Specifically,

$$d=\begin{cases}2(date/T) & \text{if } date<T/2\\ 2(1-date/T) & \text{if } date\geq T/2\end{cases} \quad (8)$$

where T is the last date in the mating season.

The fraction of $\sigma[date]$ females that actually arrive on a day is determined by the number of calling males (chorus size) and by some variable related to weather (e.g. the number of days since it has rained, *rd*). Thus, female arrival rate (*FA*) is the product of three functions: the maximum arrival rate on a given night (σ), K (a function of chorus size on a given night) and ρ (a function of the weather)

$$FA[date,rd]=\sigma[date]\times\rho[rd]\times K[date] \quad (9)$$

We assume that there is some fixed probability that it will rain on any given day, and that the potential female arrival rate decreases linearly with an increase in the number of days since it last rained. The function relating female arrival rate to ‘rain days’ is

$$\rho[rd]=\begin{cases}1-\dfrac{rd}{maxrd} & \text{if } rd\leq maxrd\\ 0 & \text{otherwise}\end{cases} \quad (10)$$

where *maxrd* is the maximum number of days without rain after which no females arrive.

Wells (1977b) suggested that in many species, the male chorus advertises the location of the breeding site to females. In addition, the number of females that arrive per calling male increases with chorus size in several species (e.g. *P. pustulosus*: Ryan et al. 1981; *B. valliceps*: Wagner & Sullivan 1992). Based on these observations, we assume that the effect of chorus size on female arrival rate ($K[date]$) is

$$K[date]=\gamma(CS[date]+\frac{\gamma_1\times CS[date]^2}{2} \quad (11)$$

where γ and γ_1 are constants. If γ_1 equals 0, the relationship is linear; if γ_1 equals 1, female arrival rate accelerates as chorus size increases. $CS[date]$ is the density of calling males when the time in the season is *date*, taken as a fraction of the number of males alive on the first day of the season. If CS is 0, we assume that a mutant male would constitute a chorus size of 1.0^{-4} if it called.

As a caller, a male’s mating success on any given night (MS_{call}) will be determined by the number of females that arrive, his age-dependent ability to attract females, and the frequency-dependent competition between satellites and callers for access to females (Wells 1977b; Perrill et al. 1978). Taken together,

$$MS_{\text{call}}[age,date,rd,\varepsilon]=$$

$$\begin{cases}\dfrac{FA[date,rd]\times\alpha[age]\times\phi[date]}{1+\iota_{\text{sat}}\times(D_{\text{sat}}[date]/D_{\text{call}}[date])} & \text{when } \varepsilon>0\\ 0 & \text{otherwise}\end{cases} \quad (12)$$

where FA is the mean female arrival rate per calling male per night, $\alpha[age]$ is relative mating ability as a function of age, ι_{sat} is relative ability of satellites to intercept females arriving at call sites ($0\leq\iota_{\text{sat}}\leq 1$), $D_{\text{call}}[date]$ and $D_{\text{sat}}[date]$ are the density of callers and satellites at the chorus, and ε is current energy state.

The numerator of equation (12) is the number of females that arrive on a territory of a male of a given age, and the denominator accounts for the reduction in mating success due to satellites. Specifically, $\iota_{\text{sat}}\times D_{\text{sat}}[date]/D_{\text{call}}[date]$ is the number of females all satellites on the territory intercept, as a fraction of the number obtained by the calling male, and $1/(1+\iota_{\text{sat}}\times D_{\text{sat}}[date]/D_{\text{call}}[date])$ is the fraction of arriving females that the calling male obtains.

Satellites share females with both callers and with other satellites (if there is more than one satellite on the territory). The mating success per satellite (MS_{sat}) is then

$$MS_{\text{sat}}[age,date,rd,\varepsilon]=MS_{\text{call}}[age,date,rd,\varepsilon]\times\iota_{\text{sat}} \quad (13)$$

Of course, if a male does not enter the chorus (i.e. if it forages or hides), its current mating success is zero.

All decisions a male makes will impact both its immediate gain in fitness and future fitness gains. Immediate payoffs are determined by the expected mating succes on a given night. Future payoffs are determined by its residual reproductive success, which in turn is affected by the change in state caused by the current decision. The recurrence equations of the dynamic programme incorporate both of these types of payoffs. For any given behaviour (‘*behav*’), the total payoff (current+future) is

$$
\begin{aligned}
&PO_{\text{behav}}[age,date,rd,\varepsilon] = MS_{\text{behav}}[age,date,rd,\varepsilon] + \\
&(1-\mu_{\text{st}}[\varepsilon])(1-\mu_{\text{behav}}[date])\left\{ P_{\text{rain}}\left\{ P_{\text{c}}\left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behav}}(PO^{*}[age,date+1,rd=0,\varepsilon+\Delta\varepsilon]) \right\} \right.\right. \\
&\quad + (1-P_{\text{c}})\left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behav}}(PO^{*}[age,T+1,rd=0,\varepsilon+\Delta\varepsilon]) \right\}\Big\} \\
&\quad + (1-P_{\text{rain}})\Big\{ P_{\text{c}}\left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behav}}(PO^{*}[age,date+1,rd+1,\varepsilon+\Delta\varepsilon]) \right\} \\
&\quad \left.\left. + (1-P_{\text{c}})\left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behav}}(PO^{*}[age,T+1,rd+1,\varepsilon+\Delta\varepsilon]) \right\}\right\}\right\} \qquad (14)
\end{aligned}
$$

where $MS_{\text{behav}}[age,date,rd,\varepsilon]$ is the current payoff if the male exhibits behaviour *behav*, which is non-zero only if the male joins the chorus (i.e. *behav* is call or satellite); $\mu_{\text{st}}[\varepsilon]$ and $\mu_{\text{behav}}[date]$ are mortality induced by starvation (a function of energetic state, ε) and mortality induced by predation conditional on behaviour *behav* being exhibited; P_{rain} is the probability of rain (*rd* is the number of days since the last rain); P_{c} is the probability that the mating season will continue at least another day; $P_{\Delta\varepsilon|\text{behav}}$ is the probability that energetic state is incremented by $\Delta\varepsilon$, given that behaviour *behav* is exhibited; PO^{*} is the optimal payoff for the sequence of decisions made on day equal $date+1$ (if the season lasts that long) or day equal $T+1$ (if the season ends), on rain-day equal 0 (if it rains) or rain-day equal $rd+1$ (if it does not rain), and at energy state $\varepsilon+\Delta\varepsilon$.

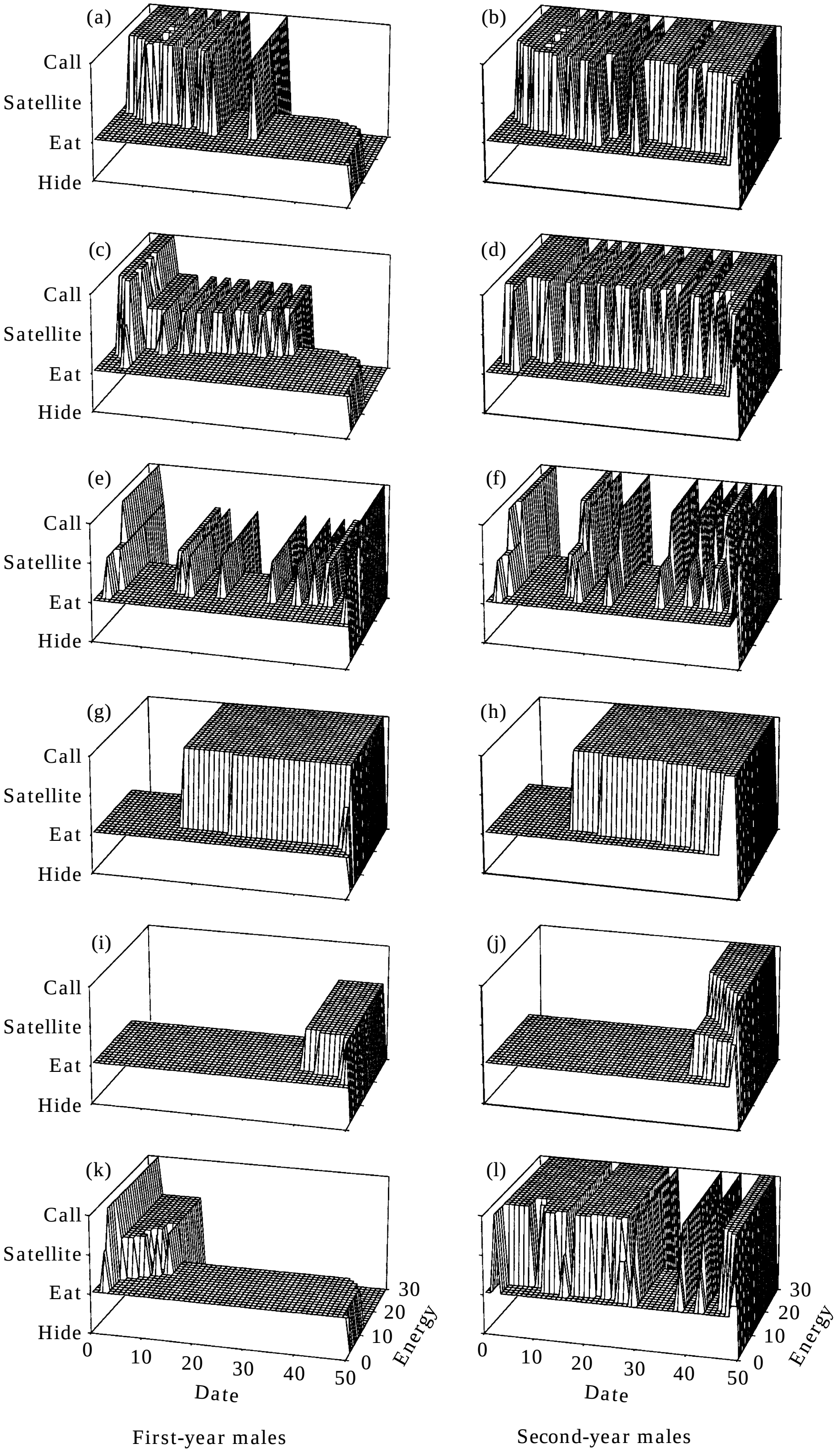
An assumption of the algorithm is that the mutant male will choose that behaviour that maximizes $PO_{\text{behav}}[age,date,rd,\varepsilon]$. Using standard dynamic programming techniques (Mangel & Clark 1988), a matrix of expected behaviour patterns at all combinations of age, date, rain-days and energy state can be generated. The matrix of behaviour patterns can then be used to estimate what a population consisting entirely of mutants will do. This is done using a simulation which essentially reverses the backward iteration used in the dynamic programme, starting the population off at age 1 and some initial frequency distribution of energy states, and ending at the last day of the season for the oldest frog in the population. This simulation provides an estimate of the expected size of each age class and frequency of occurrence of each behaviour on each day of the reproductive season.

RESULTS

The model is sufficiently complicated that it would be impractical to consider the effects of changes in all parameters and their interactions. Instead, we chose a set of parameter values that simulates a species in which adults can breed for up to 2 years and whose breeding season can extend for a maximum of 50 days each year. We then evaluate the univariate response to changes in several key parameters in the model. In the basic model, the weather is fairly stable ($P_{\text{rain}}=0.8$), and individuals experience a fairly low cost of calling ($\Delta\varepsilon_{\text{call}}=-2.5$) and low predation risk in the chorus ($\gamma_{\text{call}}=0.05$; see Table I for a full list of parameter values).

The Basic Model Without Satellites

To give some context for the influence of satellites on chorusing behaviour, we first consider a system with no satellites. Several results are particularly striking. First, all males that join a chorus should arrive in a series of clusters of waves; in other words, the chorus will be large on some days and non-existent on others, even when the weather is otherwise favourable (i.e. $rd=0$; Fig. 1a, b). The waves are caused by four factors: the energetic cost of calling, density dependence in predation risk, density dependence in female arrival rates, and frequency dependence in the ability of animals in the chorus to gain access to females. Energetic costs limit the total amount of time that males can call in a chorus; males that call several days in a row benefit from leaving the chorus to recoup their energy losses by feeding. When these energy-depleted males drop out of the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Second-year males

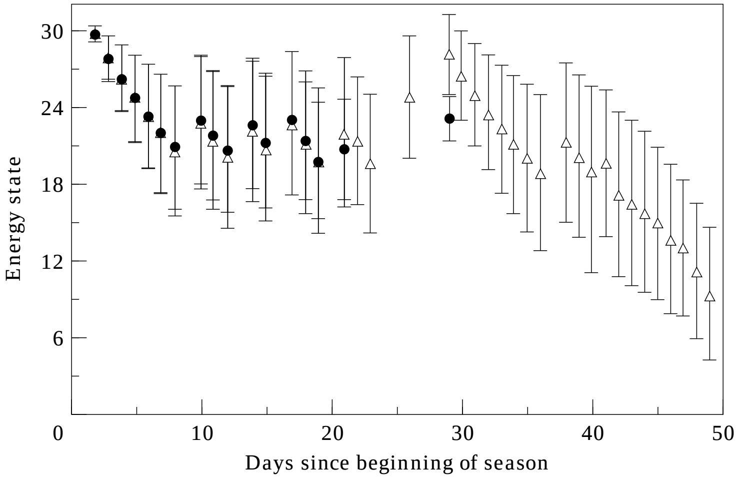


Figure 2. Mean (± SD) energy state of first- (●) and second- (△) year males in the chorus when the weather is of high quality ($rd=0$). There are no satellites in this system. Other parameter values are listed in Table I.

chorus, the density-dependent payoffs to the males remaining in the chorus are reduced; as a result, the latter males should also drop out of the chorus, even though they have sufficient energy reserves to continue. The result is a series of cycles, during which the males call a few days (and on average, lose energy reserves), then stop calling for a day or two to feed (Fig. 2). We discuss density and frequency dependence in more detail below (see Density and Frequency Dependence below).

Second, males should join a chorus only on days when the weather is most favourable ($rd=0$, which occurs on 80% of days in the season). Note that we assume a linear relationship between potential female arrival rate and rain days (rd) with an X-intercept at 4 days (i.e. no females arrive when $rd \geq 4$). Males are predicted to show a strong response to reductions in overall female availability. Even on $rd=1$, old males call only during the last 2 days of the season and first-year males never call.

Third, first-year males enter the chorus only in the beginning of the season when chorus size is maximal. As the season progresses and male density declines (as a result of predation and starvation), first-year males are less likely to join the chorus and do so only on the first day of a cycle (Fig. 3). In contrast, second-year males attend the chorus throughout the season. The difference between age classes reflects a difference in the trade-off between the cost of entering a chorus (in terms of reduced future reproductive success caused by predation and starvation risk) and the reproductive benefit accrued by calling in a chorus. Because old males have low residual reproductive value at the end of the season, the uninvadable tactic for them is to call unless their energy stores are low. For young males whose mating success will rise if they survive another year, the uninvadable tactic is to leave the chorus when the payoffs diminish because of the decline in chorus size late in the year.

Finally, first-year males with low energy stores should be more likely to feed, but second-year males with low stores should be more likely to call (Fig. 1a, b). This also reflects the difference in expected future reproductive success between the age classes.

Figure 1. Predicted behaviour exhibited by males as a function of date (days since the beginning of the season) and energy level. (a, b) No satellites. (c, d) The 'basic' model (see Table I). (e, f) High cost of calling ($\Delta\varepsilon_{call} = -7.5 \pm 2.0$). (g, h) Low probability of rain ($P_{rain}=0.2$). (i, j) High predation risk in the chorus ($\gamma_{call}=0.20$). (k, l) Low probability that season will continue the entire 50 days ($P_c=0.95$) coupled with high predation risk ($\gamma_{call}=0.20$). Parameter values for other variables are listed in Table I. The weather is of high quality for all figures ($rd=0$).

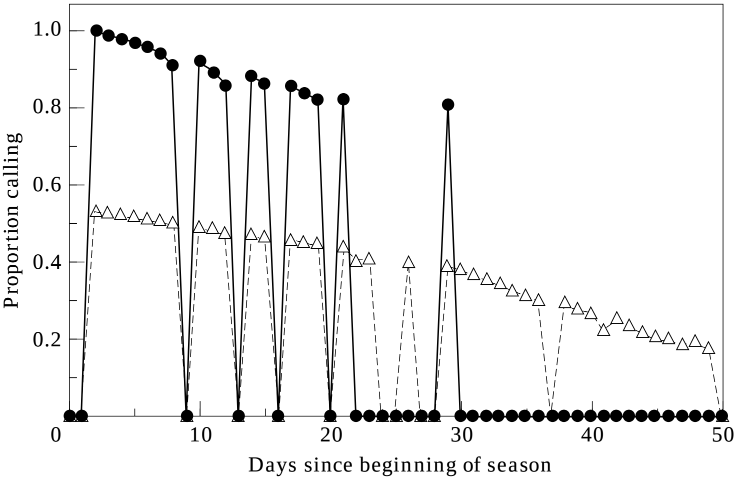


Figure 3. Relative density of first- (●) and second- (△) year calling males, given as a fraction of the number of males alive at the beginning of their first year. See Fig. 2 for details. Note that the lower values for second year males reflect mortality risks; about 50% of males die before the first day of their second mating season.

The Basic Model With Satellites

If males can choose to be satellites, the waves persist, but first-year males now switch from callers to satellites early in the season and tend to persist in the chorus longer than they would if satellites were not allowed (Fig. 1c, d). The switch to satellite occurs after the first year when males have, on average, lost about 20% of their energy reserves (Fig. 4a). Even males with high energy reserves switch to satellites, however, because their density-dependent payoffs begin to decline when energy-limited males stop calling to become satellites. Second-year males may lose substantially more than 20% of their energy reserves (Fig. 4b), but are never expected to become satellites under the conditions of the basic model.

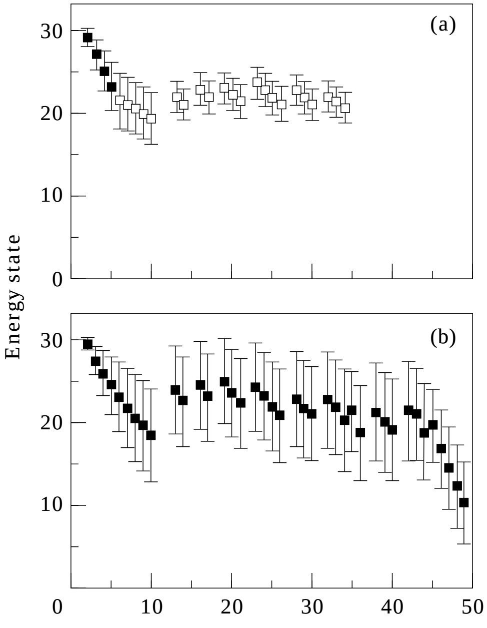


Figure 4. Mean (±SD) energy state of (a) first-year and (b) second-year males in the chorus when the weather is of high quality ($rd=0$). Parameter values are those of the 'basic model' (listed in Table I). ■: Callers; □: satellites.

Density and Frequency Dependence

There are two sources of density dependence in the model that could drive the wave pattern, predation risk and female arrival rate, and their effects on the results are markedly different. This can be illustrated by eliminating the density-dependent aspects of each selective pressure. If predation risk is treated as a constant and independent of chorus size ($\mu_{call}=0.04$ per day, $\mu_{sat}=0.008$ per day), then the waves persist. Not surprisingly, changing the level of predation will alter the outcome, but the general results are similar to those of the model with density-dependent predation.

In contrast, if female arrival rate is treated as a constant for the prolonged breeder simulated in the basic model, the system oscillates and there is no uninvadable tactic (or, at least, the algorithm used here does not find one). The lack of ESS is due to frequency dependence: the mating success of both callers and satellites decreases with an increase in satellite frequency. With a constant, density-independent female arrival rate, the mutant caller tends to have a high fitness when all other males are foraging. A population of these mutant callers then can be invaded by mutant satellites. If the frequency of satellites is high, a male could increase its fitness by foraging early in the season then joining the chorus near the end of the year. This population could then be reinvaded by callers. Of course, energetic state complicates the dynamics, but this is the essence of the problem. Adding density-dependent female arrival rates increases stability because mutant callers will not attract any females and thus will not enjoy a high fitness in a population of foragers.

The role of frequency dependence in the stability of the model can be further illustrated by eliminating it: if the payoff to callers and satellites is independent of the frequency of satellites (i.e. $MS_{call}[age,date,rd,\varepsilon] = FA[date,rd] \times \alpha[age] \times \phi[date]$, and $MS_{sat}[age,date,rd,\varepsilon] = MS_{call}[age,date,rd,\varepsilon] \times \iota_{sat}$), then the system is stable. This is true even without density-dependent female arrival rates. Thus both frequency and density dependence play significant roles in the stability and dynamics of this system.

The length of the breeding season also affects the stability of these systems. Density-independent female arrival rates are destabilizing in a prolonged breeder ($T=50$). If the breeding season is constrained to only 8 days, then the system is stable, even with density-independent female arrival rates. Season length is considered in somewhat more detail below.

Energetics

As just described, density and frequency dependence should synchronize the population through positive feedback; if some individuals are constrained to drop out of the chorus, this should cause others to drop out as well. We have implied that the energetic cost of calling is the basis for the wave patterns. This can be demonstrated in two ways, by altering the cost of attending the chorus and by changing the weather such that the energetic costs of calling is less relevant to fitness.

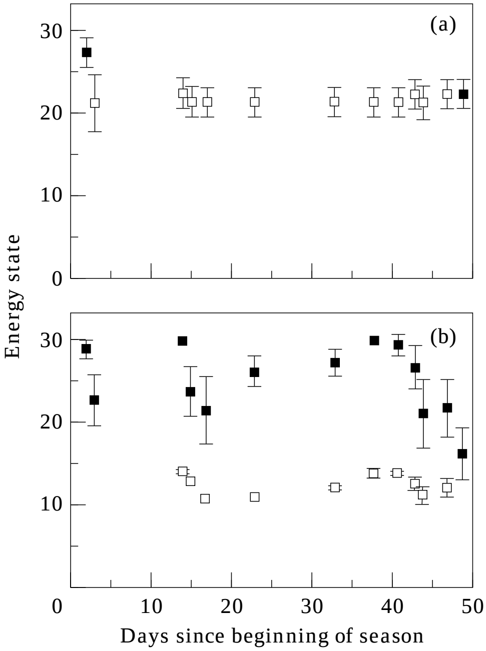
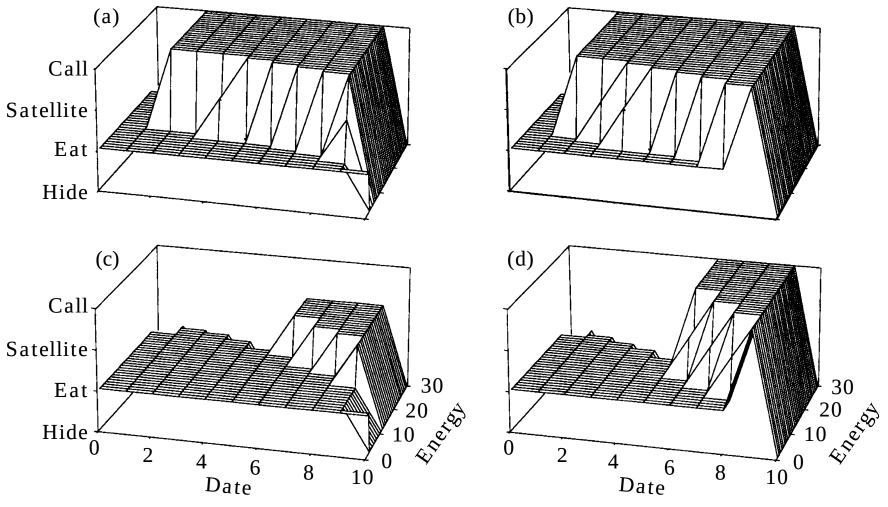


Figure 5. Mean (±SD) energy state of (a) first- and (b) second-year males with a high cost of calling ($\Delta\varepsilon_{call} = -7.5$) when the weather is of high quality ($rd=0$). Other parameter values are listed in Table I. ■: Callers; □: satellites.

If the cost of calling is doubled ($\Delta\varepsilon_{call} = -7.5 \pm 2.0$), the waves are less frequent and of shorter duration (Fig. 1e, f). Another change in the ESS is that old males with low energy levels should switch to satellites, but with the basic model ($\Delta\varepsilon_{call} = -2.5 \pm 2.0$), only young males become satellites. This underscores the fact that there can be several classes of satellites, and that different selective pressures can affect the expression of this behaviour in the different classes. When the energetic costs of calling are high, young males are more likely to be satellites when they suffer a low mating success (compared to older males) and high predation risk (which jeopardizes future reproductive success), but older males with low energy reserves are more likely to become satellites (Fig. 5a, b).

When the energetic cost of attendance is low ($\Delta\varepsilon_{call} = -0.5 \pm 2.0$, $\Delta\varepsilon_{sat} = 0 \pm 0.3$), then there are no waves. First-year males above some



First-year males

Second-year males

Figure 6. Predicted behaviour exhibited by males as a function of date (days since the beginning of the season) and energy level when the reproductive season is constrained to 10 days. (a, b) $rd=0$. (c, d) $rd=1$. Other parameter values are listed in Table I.

minimum energy level attend the chorus as satellites every day during the season when the weather is optimal (i.e. $rd=0$), and second-year males call all season long.

Even with a high cost of calling, environmental factors may reduce the impact of energetics on chorus attendance. In species where female arrival is sporadic, for example occurring only on rainy nights in a relatively dry climate, there may be sufficient time between rains for males to recoup energetic losses, irrespective of the energetic cost of calling. Under the conditions simulated here, a change in the probability of a high-quality day (P_{rain}) from 0.8 to 0.2 eliminates the wave pattern (Fig. 1g, h). Thus, if the energetic cost of calling is high enough, some respite is necessary for the chorusing males. This respite can be intrinsically generated by cyclical chorusing, or extrinsically generated by environmental conditions that only sporadically favour calling.

Season Length

Although the length of the season is potentially 50 days in the basic model, several factors can cause the season to be substantially shorter. In particular, a high predation risk ($\gamma_{\mathrm{call}}=0.20$) or a high satellite mating ability ($\iota_{\mathrm{sat}}=0.8$) will truncate the season, essentially turning a prolonged breeder (sensu Wells 1977b) into an explosive breeder (e.g. Fig. 1i, j).

The results suggest that young males either drop out of the chorus, or play the more conservative satellite tactic in the chorus, when future reproductive success is high relative to current reproductive success. Future reproductive success, in turn, will be affected by mortality risks and by weather patterns that limit the length of the season. The latter could arise in species that use highly ephemeral breeding habitats, for which the mating season could be limited to less than a week. Results obtained in a model in which the breeding season is extrinsically constrained to 10 days due to weather differ from those obtained in the basic model when conditions cause intrinsic constraints on season length. With extrinsic constraints, virtually all males call when the weather is of high quality ($rd=0$; Fig. 6a, b). Also, more males enter the chorus on low-quality days (e.g. $rd=1$), and young males tend to become satellites on these days (Fig. 6c, d). Thus, all else being equal, anurans constrained to short seasons because of extrinsic environmental conditions should have fewer satellites than anurans for which the season is not so constrained. Similar results are derived when life span is manipulated:

all else being equal, iteroparous species should have a higher proportion of satellites in choruses than semelparous species.

These results underscore two important aspects of dynamic games. The first is that the ESS tactic is not necessarily the tactic that maximizes individual fitness. For example, if predation risk to calling males is high, chorus formation is predicted to be deferred to late in the potential reproductive season, even though calling males in such a ‘late chorus’ should experience even higher predation risk than they would if they were to attend an ‘early chorus’. The higher predation risk results from the density-dependent nature of predation in choruses. Fewer males should be alive in the population later in the season due to the cumulative effect of predation on foragers. In addition, delayed chorusing behaviour is expected even though there is a finite chance that the season will end prematurely (the probability that the season continues every day, P_c, is 0.99 per day).

The second important aspect of these games is that constraints imposed on certain members of the population may affect the tactics used by all other members of the population. Under the conditions simulated here, second-year males have no future reproductive success at the end of the reproductive season, and thus are forced to call at the end of the season if they are to realize any fitness gains. An alternative way of viewing the situation is that the cost of calling for these males is low, so they have little to lose at the end of the season. Younger males are able to parasitize older males by employing the satellite tactic, but when predation risk is high, this arrangement is evolutionarily stable only late in the season. The pattern can be reversed when the season is likely to end prematurely due to a sudden change in weather ($P_c = 0.95$). Under these conditions, young males enter as satellites early then drop out of the chorus altogether, whereas older males call all season (Fig. 1k, l).

DISCUSSION

Numerous hypotheses have been suggested for why males employ satellite tactics to obtain mates. Most focus on four factors: density-dependent payoffs to satellites and callers in the chorus (Greenfield & Shelly 1985; Ovaska & Hunte 1992; Rowell & Cade 1993), satellite behaviour as a mechanism of avoiding the high metabolic cost of calling (Forester & Lykens 1986; Sullivan 1987; Arak 1988; Krupa 1989; Ovaska & Hunte 1992), satellite behaviour as a mechanism of avoiding the high predation risk suffered by calling males (Forester & Lykens 1986; Perrill & Magier 1988; Green 1990), and satellite behaviour as an alternative reproductive tactic available to unattractive males that face reduced fitness as callers (a conditional ESS: Greenfield & Shelly 1985; Forester & Lykens 1986; Arak 1988; Krupa 1989; Ovaska & Hunte 1992).

Evidence from natterjack toads, *B. calamita*, suggests that satellites are not energetically constrained, but instead tend to be smaller than callers (Arak 1988), supporting the hypothesis that satellites represent a conditional ESS. Arak (1988) developed an ESS model to determine when males should become satellites instead of calling, a problem somewhat different than the one we have addressed. His conclusion was that a male should become a satellite when it is only half as loud as its nearest neighbour. Unfortunately, this model did not include the effect of energetic state, nor did it include the effects of female arrival rate.

The advantage of a dynamic game approach, as used here, is the simultaneous evaluation of both energetics and conditional tactics. Our analyses show that for prolonged breeders in habitats in which favourable conditions for reproduction are relatively continuous during the season, male reproductive decisions should depend on energetic state and should be conditional on age or size, if the cost of calling is relatively high. Alternatively, energetic state should be less important for species that have prolonged breeding seasons in which favourable breeding opportunities are episodic and brief due to weather variation or for species that breed explosively in ephemeral habitats. Variation in the intensity of breeding activity due to weather conditions (temperature and rainfall) has been documented in several anuran species with prolonged breeding seasons (e.g. *P. pustulosus*: Green 1990; *Hyperolius marmoratus*: Dyson et al. 1992; *B. calamita*: Tejedo 1993) but not in others (e.g. 16 species described by Crump 1974; *Hyla cinerea*: Garton & Brandon 1975; *H. versicolor*: Fellers 1979; Gerhardt et al. 1987; *H. chrysoscelis*: Ritke et al. 1992). For both types of prolonged breeders, the number of consecutive days of chorus attendance by individual males is typically low relative to the length of the breeding season (e.g. Fellers 1979; Goodwin & Roble 1983; Dyson et al. 1992; Tejedo 1992; Murphy 1994). Although we recognize that many variables can affect chorus attendance, our model predicts that energy limitations should be relatively more important in limiting chorus attendance for prolonged breeders than for explosive breeders.

In addition to fluctuations in chorus size caused by extrinsic factors such as varying weather patterns, our model shows that chorus size may also fluctuate as a result of more intrinsic factors. If the cost of calling is relatively high and if female arrival rate increases with chorus size, then the chorus should show waves of activity interrupted by days when most males forage. This wave pattern should be most pronounced in prolonged breeders. The basis of the wave pattern is a reduction in fitness caused by low energy stores, coupled with the positive density dependence caused by chorus-size related female arrival rates. In essence, density-dependent payoffs should cause most males in the population to coordinate their chorus activity. Several studies clearly show a high variance in chorus size for prolonged breeders (e.g. *H. versicolor*: Fellers 1979; *R. catesbeiana*: R. D. Howard, unpublished data; *H. rosenbergi*: Kluge 1981). However, we need much more detailed information on chorus attendance to evaluate these predictions fully.

The degree to which energy state determines male reproductive decisions also depends on the time scale over which energy is lost and regained. Our model assumes that calling males lose from 5 to 25% of their energy reserves during a night of calling, and can only recoup this loss over the course of a few days. Daily and seasonal weight loss have been demonstrated for calling males of most species with prolonged breeding seasons (e.g. *R. clamitans*: Wells 1978; *Ranidella signifera* and *R. parinsignifera*: MacNally 1981; *B. calamita*: Arak 1983; *U. rugosa*: Robertson 1986; *Rana virgatipes*: Given 1988; *B. rangeri*: Cherry 1993; *H. gratiosa*: Murphy 1994, but see Sullivan 1989a for *B. woodhousii*; Howard 1984 for *R. catesbeiana*).

Our model predicts that female arrival rate is a critical determinant of male chorus attendance as well as the mating tactics used by attending males. Studies on a number of anuran species have found positive relationships between the number of arriving females and the number of males in a chorus (e.g. Ryan et al. 1981; Woodward 1984; Gerhardt et al. 1987; Hoglund & Robertson 1987; Odendall & Iwasa 1987; Dyson et al. 1992; Wagner & Sullivan 1992; Tejedo 1993). Few studies have detected an increase in the number of females per male with increasing chorus size (e.g. Ryan et al. 1981; Wagner & Sullivan 1992; Tejedo 1993); some studies could detect no such relationship (e.g. Odendall & Iwasa 1987; Krupa 1989), and one study found fewer females per male in larger choruses (Sullivan 1986). Typically, a positive relationship between the number of females and males attending choruses is presumed to result from use of common environmental cues by the sexes. The effect of female arrival rates on the male's decision to become a caller or satellite has only rarely been addressed. Waltz (1982) predicted that satellite tactics should be favoured if females are synchronous in arrival times; however, Krupa (1989) could find no relationship between the frequency of satellites and either the total number of females in the chorus or the ratio of males to females in *B. cognatus*.

Several aspects of female arrival rates should be important in a male's choice of reproductive tactic: the degree to which long-term weather patterns limit the total duration of the breeding season (T in our model), the effect of short-term changes in the weather (such as rainfall, temperature, or light levels) on female arrival rates, and the density-dependent relationships between chorus size and female behaviour.

Breeding season length differs markedly among species, ranging from 1 day to nearly a full year (Crump 1974; Wells 1977b; Sullivan 1989b). For some species, short seasons are clearly constrained by weather patterns (e.g. desert anurans that use highly ephemeral ponds; Sullivan 1989b). The results from the model suggest that satellites should be less frequent in the latter species than in more prolonged breeders, assuming that other factors such as predation risk and short-term factors governing female arrival rates are similar between explosive and prolonged breeders. More information is needed to evaluate this prediction.

In addition to extrinsic constraints limiting breeding season length, explosive breeding may also result from intrinsic forces. Species such as the American toad, *B. americanus*, have extremely short breeding seasons (only a few days per year; Howard 1988), yet often breed in relatively permanent habitats. One possible explanation for their contracted breeding season is high predation pressure on adults; our results show that high predation rates can significantly reduce breeding season length. Unfortunately, not enough is known about this system to evaluate this possibility.

A number of authors have suggested that satellites represent males with low mate-attraction abilities (i.e. young or small) that become satellites as a means of making the best of a bad job (Parker's 1984 'phenotype limited' ESS; e.g. Arak 1983, 1988; Howard 1984; Forester & Lykens 1986; Robertson 1986; Krupa 1989). However, not all species have satellites that are demonstrably less attractive. For example, no size differences were found between callers and satellites in *A. crepitans* (Perrill & Magier 1988), *B. woodhousii* (Sullivan 1989a), *H. chrysoscelis* and *Pseudacris triseriata* (Roble 1985). These data support our predictions that two categories of satellite males could exist: young males and old males that were callers but depleted their energy reserves. Observations on several species support this prediction (e.g. *R. clamitans*: Wells 1977a; *U. rugosa*: Robertson 1986; *E. johnstonei*: Ovaska & Hunte 1992).

Our results further suggest that different selective pressures should determine whether males in these different categories choose to become satellites. The advantages of calling are that it draws females into the chorus and increases the attractiveness of males to females, compared to being a satellite. The disadvantages of calling are that it is risky and energetically expensive behaviour (Ryan et al. 1981; Taigen & Wells 1985). An additional disadvantage to calling is that the females attracted to callers can be intercepted by satellite males (see Perrill et al. 1978; Gerhardt et al. 1994); these satellites suffer lower predation risk and expend less energy than callers. For first-year males, the balance between the advantages and disadvantages of calling must be placed in the context of expected future reproducive success. Young males should tend to be satellites because by doing so they enjoy increased survival to the next breeding season when mate attraction ability should increase. In contrast, whether old males choose to become satellites should more strongly depend on the immediate consequences of chorus attendance. Older males are expected to adopt satellite tactics more often in species in which calling costs are high and the mating success of satellite males approximates that of calling males.

The frequency- and density-dependent attributes of female arrival rate are critical to the stability of the model. The system is stable if female arrival rate has a zero intercept and increases with chorus size. However, if female arrival rate is independent of chorus size, or, more generally, if female arrival rate as a function of chorus size has a non-zero intercept, then under some circumstances the system is unstable if the payoffs to callers and satellites is a function of the frequency of satellites. Such satellite frequency-dependent payoffs are likely to be common, because satellites intercept females attracted to calling males. Thus female arrival rate relative to the number of calling males is a key variable. As with other traits, species appear to differ markedly in this relationship. As Wells (1977b) suggested, positive density dependence (more females attracted to larger choruses of calling males) occurs in some species (e.g. *Physalaemus pustulosus*: Ryan et al. 1981; *Hyperolius marmoratus*: Dyson et al. 1992; *B. valliceps*: Wagner & Sullivan 1992; see also Greenfield & Shelly 1985, for an example in insects). Positive density dependence is not universal, however. In *B. woodhousii*, the operational sex ratio (number of females per calling male) actually decreases with chorus size (Sullivan 1986). Several other species have been described where female arrival rates are poorly correlated with male chorus size, but these species also tend to be explosive breeders (Wells 1977b). We know of no prolonged breeders with inverse density dependence. One intriguing possibility is that the inherent instability in the frequency of callers and satellites in prolonged breeders reduces the chance that negative density dependence will evolve in these systems.

Our model treats male mating behaviour as a dichotomous choice between calling and being a satellite. Although this model is appropriate for many species, a third alternative, searching, is exhibited in some explosive breeders (e.g. Wells 1977b; Arak 1988; Woolbright et al. 1990; Tejedo 1992). The addition of searching makes an already complicated system all the more so. The behaviour clearly depends on male density, being exhibited almost exclusively in high-density choruses (e.g. Arak 1983). Unfortunately, the relationship between the frequency of this behaviour and female arrival rate is poorly documented.

Given that searchers may call even more than stationary males in some species (e.g. *R. sylvatica*: Woolbright et al. 1990), there is likely to be a relationship between the density of searchers and female arrival rates.

In many explosive breeders, there seems to be a dichotomy between calling and searching, as opposed to the dichotomy between caller and satellite as we have modelled male reproductive tactics in this paper. Perhaps the caller/searcher dichotomy results because extreme female synchrony and the lack of a clear differential in mate attraction ability of males favours males that ‘play the field’ rather than parasitizing the ability of specific males to attract females (Arak 1988). These relationships need to be quantified, the relative mating success of searchers (both calling and non-calling searchers), stationary callers and their associated satellites needs to be quantified, in addition to the energetics of this behaviour and potential size-dependent mating success.

The recent introduction of dynamic optimization to the study of behaviour (Mangel & Clark 1988) permits the evaluation of behavioural alternatives in a much more realistic manner than has previously been possible. For example, our dynamic game includes aspects of sequential dependence (e.g. a weighing of future fitness benefits on current decisions), state dependence, frequency dependence and density dependence in the payoffs to alternative mating tactics in anurans, and allows us to evaluate the relative importance of these conditions and how they interact. Many excellent empirical studies have addressed specific parts of this problem. Hopefully our results will point out that studies of somewhat broader scope are worth undertaking. We need a better understanding of the factors governing female arrival rates and factors governing both the density- and frequency-dependent attributes of male reproductive trade-offs. With dynamic optimization, we now have the tools to synthesize the theoretical framework of this broader scope.

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REFERENCES

Arak, A. 1983. Male–male competition and mate choice in anuran amphibians. In: *Mate Choice* (Ed. by P. P. G. Bateson), pp. 181–210. Cambridge: Cambridge University Press.

Arak, A. 1984. Sneaky breeders. In: *Producers and Scroungers* (Ed. by C. J. Barnard), pp. 154–194. London: Croom Helm.

Arak, A. 1988. Callers and satellites in the natterjack toad: evolutionarily stable decision rules. *Anim. Behav.*, **36,** 416–432.

Bucher, T. L., Ryan, M. J. & Bartholomew, G. A. 1982. Oxygen consumption during resting, calling, and nest building in the frog *Physalaemus pustulosus. Physiol. Zool.*, **55,** 10–22.

Cherry, M. I. 1993. Sexual selection in the raucous toad, *Bufo rangeri. Anim. Behav.*, **45,** 359–373.

Crump, M. L. 1974. Reproductive strategies in a tropical anuran community. *Misc. Publs Mus. nat. Hist. Univ. Kans.*, **61,** 1–68.

Dunbar, R. I. M. 1982. Intraspecific variations in mating strategy. In: *Perspectives in Ethology, Vol. 5* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 385–431. New York: Plenum.

Dyson, M. L., Passmore, N. I., Bishop, P. J. & Henzi, S. P. 1992. Male behavior and correlates of mating success in a natural population of African painted reed frogs (*Hyperolius marmoratus*). *Herpetologica,* **48,** 236–246.

Fellers, G. M. 1979. Mate selection in the gray treefrog, *Hyla versicolor. Copeia,* **1979,** 286–290.

Forester, D. C. & Lykens, D. V. 1986. Significance of satellite males in a population of spring peepers (*Hyla crucifer*). *Copeia,* **1986,** 719–724.

Garton, J. S. & Brandon, R. A. 1975. Reproductive ecology of the green tree frog, *Hyla cinerea*, in southern Illinois (Anura: Hylidae). *Herpetologica,* **31,** 150–161.

Gerhardt, H. C., Daniel, R. E., Perrill, S. A. & Schramm, S. 1987. Mating behaviour and male mating success in the green treefrog. *Anim. Behav.*, **35,** 1490–1503.

Gerhardt, H. C., Dyson, M. L., Tanner, S. D. & Murphy, C. G. 1994. Female treefrogs do not avoid heterospecific calls as they approach conspecific calls: implications for mechanisms of mate choice. *Anim. Behav.*, **47,** 1323–1332.

Given, M. F. 1988. Growth rate and the cost of calling activity in male carpenter frogs, *Rana virgatipes. Behav. Ecol. Sociobiol.*, **22,** 153–160.

Goodwin, G. J. & Roble, S. M. 1983. Mating success in male treefrogs, *Hyla chrysoscelis* (Anura: Hylidae). *Herpetologica,* **39,** 141–146.

Gosling, L. M. & Petri, M. 1990. Lekking in topi: a consequence of satellite behaviour by small males at hotspots. *Anim. Behav.*, **40,** 272–287.

Grafe, T. U., Schmuck, R. & Linsemair, K. E. 1992. Reproductive energetics of the African reed frogs, *Hyperolius viridiflavus* and *Hyperolius marmoratus*. *Physiol. Zool.*, **65,** 153–171.

Green, A. J. 1990. Determinants of chorus participation and the effects of size, weight, and competition on advertisement calling in the tungara frog, *Physalaemus pustulosus* (Leptodactylidae). *Anim. Behav.*, **39,** 620–638.

Greenfield, M. D. & Shelly, T. E. 1985. Alternative mating strategies in a desert grasshopper: evidence of density-dependence. *Anim. Behav.*, **33,** 1192–1210.

Gross, M. R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.*, **60,** 1–26.

Hoglund, J. & Robertson, J. G. M. 1987. Random mating by size in a population of common toads (*Bufo bufo*). *Amphib. Rept.*, **8,** 321–330.

Houston, A. I. & McNamara, J. M. 1982. A sequential approach to risk-taking. *Anim. Behav.*, **30,** 1260–1261.

Houston, A. I. & McNamara, J. M. 1987. Singing to attract a mate: a stochastic dynamic game. *J. theor. Biol.*, **129,** 57–68.

Houston, A. I. & McNamara, J. M. 1988. Fighting for food: a dynamic version of the hawk-dove game. *Evol. Ecol.*, **2,** 51–64.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana. Evolution*, **32,** 850–871.

Howard, R. D. 1984. Alternative mating behaviors of young male bullfrogs. *Am. Zool.*, **24,** 397–406.

Howard, R. D. 1988. Sexual selection on male body size and mating behaviour in American toads, *Bufo americanus. Anim. Behav.*, **36,** 1796–1808.

Jaeger, R. G. 1976. A possible prey-call window in anuran auditory perception. *Copeia*, **1976,** 833–834.

Kluge, A. G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Misc. Publs Mus. Zool. Univ. Mich.*, **60,** 1–170.

Krupa, J. J. 1989. Alternative mating tactics in the great plains toad. *Anim. Behav.*, **37,** 1035–1043.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68,** 619–640.

Lucas, J. R. 1983. The role of foraging time constraints and variable prey encounter in optimal diet choice. *Am. Nat.*, **122,** 191–209.

Lucas, J. R. 1985. Time constraints and diet choice: different predictions from different constraints. *Am. Nat.*, **126,** 680–705.

Lucas, J. R. & Walter, L. R. 1991. When should chickadees hoard food? Theory and experimental results. *Anim. Behav.*, **41,** 579–601.

MacNally, R. C. 1981. On the reproductive energetics of chorusing males: energy depletion profiles, restoration and growth of two sympatric species of *Ranidella* (Anura). *Oecologia* (*Berl.*), **51,** 181–188.

Mangel, M. & Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, New Jersey: Princeton University Press.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Murphy, C. G. 1994. The determinants of chorus tenure in barking treefrogs (*Hyla gratiosa*). *Behav. Ecol. Sociobiol.*, **34,** 285–294.

Nee, S. & May, R. M. 1993. Population-level consequences of conspecific brood parasitism in birds and insects. *J. theor. Biol.*, **161,** 95–109.

Odendall, F. J. & Iwasa, Y. 1987. Operational sex ratio in *Ranidella signifera* and *Ranidella riparia* (Anura: Leptodactylidae). *Copeia*, **1987,** 1025–1028.

Ovaska, K. & Hunte, W. 1992. Male mating behavior of the frog *Eleutherodactylus johnstonei* (Leptodactylidae) in Barbados, West Indies. *Herpetologica*, **48,** 40–49.

Parker, G. A. 1984. Evolutionarily stable strategies. In: *Behavioural Ecology: an Evolutionary Approach*. 2nd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 30–61. Oxford: Blackwell Scientific Publications.

Perrill, S. A. 1984. Male mating behavior in *Hyla regilla. Copeia*, **1984,** 727–732.

Perrill, S. A. & Magier, M. 1988. Male mating behavior in *Acris crepitans. Copeia*, **1988,** 245–248.

Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1978. Sexual parasitism in the green tree frog (*Hyla cinerea*). *Science*, **200,** 1179–1180.

Read, A. F. & Harvey, P. H. 1993. Evolving in a dynamic world. *Science*, **260,** 1760–1762.

van Rhijn, J. G. 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax* (L.). *Behaviour*, **47,** 153–229.

Ritke, M. E., Babb, J. G. & Ritke, M. K. 1992. Temporal activity in the gray treefrog (*Hyla chrysoscelis*). *J. Herpetol.*, **26,** 107–111.

Robertson, J. G. M. 1986. Male territoriality, fighting, and assessment of fighting ability in the Australian frog, *Uperoleia rugosa. Anim. Behav.*, **34,** 763–772.

Roble, S. M. 1985. Observations on satellite males in *Hyla chrysoscelis*, *Hyla picta*, and *Pseudacris triseriata. J. Herpetol.*, **19,** 432–436.

Rowell, G. A. & Cade, W. H. 1993. Simulation of alternative male reproductive behavior: calling and satellite behavior in field crickets. *Ecol. Modell.*, **65,** 265–280.

Ryan, M. J., Tuttle, M. D. & Taft, L. K. 1981. The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.*, **8,** 273–278.

Ryser, J. 1989. Weight loss, reproductive output, and the cost of reproduction in the common frog, *Rana temporaria. Oecologia* (*Berl.*), **78,** 264–268.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Sullivan, B. K. 1986. Intra-population variation in the intensity of sexual selection in breeding aggregations of Woodhouse's toad (*Bufo woodhousei*). *J. Herpetol.*, **20,** 88–90.

Sullivan, B. K. 1987. Sexual selection in woodhouse's toad (*Bufo woodhousei*). III. Seasonal variation in male mating success. *Anim. Behav.*, **35,** 912–919.

Sullivan, B. K. 1989a. Mating system variation in Woodhouse's toad (*Bufo woodhousei*). *Ethology*, **83,** 60–68.

Sullivan, B. K. 1989b. Desert environments and the structure of anuran mating systems. *J. arid Environ.*, **17,** 175–183.

Taigen, T. L. & Wells, K. D. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. comp. Physiol. B.*, **155,** 163–170.

Tejedo, M. 1992. Large male mating advantage in natterjack toads, *Bufo calamita*: sexual selection on energetic constraints? *Anim. Behav.*, **44,** 557–569.

Tejedo, M. 1993. Do male natterjack toads join larger breeding choruses to increase mating success? *Copeia*, **1993,** 75–80.

Wagner, W. E., Jr & Sullivan, B. K. 1992. Chorus organization in the Gulf Coast toad (*Bufo valliceps*): male and female behavior and the opportunity for sexual selection. *Copeia*, **1992,** 647–658.

Waltz, E. C. 1982. Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behav. Ecol. Sociobiol.*, **10,** 75–83.

Wells, K. D. 1977a. Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology*, **58,** 750–762.

Wells, K. D. 1977b. The social behaviour of anuran amphibians. *Anim. Behav.*, **25,** 666–693.

Wells, K. D. 1978. Territoriality in the green frog (*Rana clamitans*): vocalizations and agonistic behaviour. *Anim. Behav.*, **26,** 1051–1063.

Woodward, B. D. 1984. Arrival to and location of *Bufo woodhousei* in the breeding pond: effect on the operational sex ratio. *Oecologia* (*Berl.*), **62,** 240–244.

Woolbright, L. L., Greene, E. J. & Rapp, G. C. 1990. Density-dependent mate searching strategies of male woodfrogs. *Anim. Behav.*, **40,** 135–142.