4 · Modeling alternative mating tactics as dynamic games

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CHAPTER SUMMARY

Alternative reproductive tactics may result from various causal mechanisms. This is relevant for the theoretician because the mathematical approach used to address the evolution of alternative mating tactics will be affected by the causal basis of the differential expression of these behavior patterns between (and within) individuals. In this chapter, we restrict our focus to alternative male mating tactics that are strictly controlled by short-term behavioral decisions. Based on a variation of the Lucas and Howard (1995) dynamic game-theory model, we show that a detailed understanding of five properties of a system with alternative reproductive tactics is important in understanding the evolutionary trade-offs associated with the choice among alternative mating tactics. These properties include (1) physiological or morphological state and how state is affected by the tactic chosen, (2) environmental conditions, (3) frequency- and (4) density-dependent attributes of the pay-offs derived from each tactic, and (5) time constraints that either directly affect the expression of a mating tactic or affect the pay-offs derived from those tactics. These five properties should be considered simultaneously, and we demonstrate how this can be done within the framework of a dynamic game. The model is extended to consider the evolution of graded signals. Our model suggests that the prediction of Proulx *et al.* (2002) that older males should have more honest signals is sensitive to assumptions made about environmental conditions and time constraints on future success. We end with a discussion of the level of detail that should be built into models.

4.1 INTRODUCTION

Nothing in life is simple. A basic decision when modeling any biological phenomenon is to ignore complexities or incorporate them. Our initial attempts to model alternative mating tactics (ARTs) in anurans as a dynamic game incorporated many of the complexities of caller/satellite dynamics (Lucas and Howard 1995, Lucas *et al.* 1996). We quickly realized that, despite a huge literature on mating behavior and alternative male mating tactics in anurans (see reviews in Gerhardt and Huber 2002, Shuster and Wade 2003), no single study existed that provided all the information necessary to parameterize our model. Furthermore, certain components of the model (e.g., many aspects of female behavior) were poorly known for all species. As a result, our primary objective in this chapter is to call for more complete empirical studies of alternative mating tactics, particularly for species where the choice of an alternative mating tactic is behaviorally mediated. Our approach is to provide a fairly synoptic view of certain types of male mating tactics and to illustrate why we need more information on various aspects of mating behavior. We begin by describing how alternative mating behavior patterns are classified in terms of their underlying causation. We then narrow the scope of our investigation to consider one class of alternative mating tactics, those in which behaviors are dynamically regulated by each male, and focus on caller/satellite tactics.

4.2 UNDERLYING BASES FOR ARTs: GENETIC, DEVELOPMENTAL, AND BEHAVIORAL

Shuster and Wade (2003) described three general classes of alternative mating behavior. One class represents mating *strategies* that are simple Mendelian traits that breed true (i.e., are 100% transmitted from parent to offspring), and the other two represent mating *tactics* that are controlled, at least in part, by environmental factors or environmentally induced physiological factors. These classes can be differentiated by the timescale over which they develop (Shuster and Wade 2003). As we point out later in this section, the classification is incomplete because a number of mating

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tactics fall under multiple classes. Nonetheless, the classification is useful because it at least underscores potential differences in causal mechanisms governing the expression of these traits.

Mating *strategies* result from genetic differences between individuals, and they are therefore fixed in an individual at birth. The best example of this is the existence of three male morphs of the isopod *Paracerceis sculpta* (Shuster and Guthrie 1999). In this species, genetic differences determine the difference between territorial males, satellite males, and males that show a third, intermediate tactic.

Two classes of mating *tactics* have been described. One occurs when males undergo a developmental switch at some ontogenetic stage that determines their use of a specific mating tactic when they are adults. Such tactics most likely result from a genotype × environment interaction, as both genetic and environmental factors underlie trait expression (Taborsky 1998, Garant *et al.* 2002). For example, rapidly growing males develop into a sneaker morph, whereas more slowly growing males become dominant morphs in both coho salmon (Gross 1984, 1985) and Atlantic salmon (Hutchings and Myers 1994). Similarly, horn morphology in male dung beetles and the correlated alternative mating tactics employed by these adults are determined by larval feeding history (Moczek *et al.* 2002). Theoretically, the extent to which the switch is genetically controlled will affect the relative dynamics of the evolution of these traits. The basis of the switch will also determine, in part, how these systems are modeled.

The second class of alternative mating tactics includes males that can switch rapidly between tactics. In this chapter, we refer to tactics in this class as being under behavioral control. For example, green tree frogs can switch from satellites to callers in a matter of seconds (Perrill *et al.* 1978).

This classification follows Shuster and Wade (2003). A similar classification has been discussed by Taborsky (1998). Taborsky (1998) enumerated three dimensions of ARTs: *determination*, *plasticity*, and *selection*. Determination refers to whether the ART is controlled strictly by genetic differences between individuals, by a genotype × environment interaction, or by prevailing environmental conditions. Plasticity describes whether the ART is fixed for life, or changes once during ontogeny, or changes multiple times on a momentary timescale. Selection stipulates whether alternative traits stabilize at equal fitness or whether they reflect a disparity in quality between individuals. Under this terminology, *strategies* are fixed, genetically determined ARTs. *Tactics* are environmentally determined and can either be plastic or fixed (i.e., as a result of a genotype × environment interaction). While the classifications by Shuster and Wade (2003) and Taborsky (1998) are similar, Taborsky (1998) explicitly describes more complex origins of ARTs than those implied by Shuster and Wade's (2003) three categories. For example, *determination* may include both genetic and environmental inputs.

Strikingly different mathematical approaches are used to study these three classes of alternative mating behavior. Mendelian genetics is used to model alternative mating strategies that are determined by one or a few loci and that breed true. This entails an analysis of the reproductive fitness contributed by each allele that codes for a specific mating strategy (e.g., Shuster and Wade 2003). Developmentally based tactics are better studied by using life-history theory (e.g., Roff 1992, Stearns 1992, Charnov 1993) or, more narrowly, the theory of reaction norms (Schlichting and Pigliucci 1998). For alternative mating strategies (i.e., strictly Mendelian traits), we expect equal fitness of individuals expressing each strategy. If the alternative tactic is a developmental phenomenon, understanding the basis of the developmental switch is critical. For example, assume that the tactic employed by males results from differences among individuals in juvenile growth rate. If the tactic employed by a male results from genetically determined differences among individuals in juvenile growth rate, then we might expect equal fitness across tactics. However, Gross and Repka (1998) showed that when individuals that express different ARTs do not breed true, unequal fitness of the different morphs could be stable. (Simply put: if the most successful morph generates offspring that express the less successful morphs, then both morphs can be maintained in the population irrespective of differences between morphs in lifetime reproductive success.) Also, if developmental rates are determined by stochastic components in the environment such that any individual can express any of the possible growth rates exhibited in the population, then there is no expectation of equal fitness (see Dawkins 1980, Gross 1996). In either case, we would think of the mating tactic as a general rule: if growth rate is x, then become a satellite/sneaker; if growth rate is y, then become a territory owner. This rule may show some variation between habitats; if so, it should be treated as a reaction norm. The question then becomes: which rule is evolutionarily stable, in the sense that it cannot be invaded by an alternative rule (see Gross and Repka 1998)?

Finally, when alternative mating tactics are under behavioral control, the problem becomes one of economic decision-making. Game theory (Maynard Smith 1982, Parker 1984, Dugatkin and Reeve 1998) is one approach that could be used to study this class of mating tactics. A more robust but more complex approach is dynamic game theory (Houston and McNamara 1999, Clark and Mangel 2000). Dynamic games involve two components: dynamic optimization and game-theoretic pay-offs. The dynamic optimization component of the model has several functions. It acknowledges the potential for changes in some state variable to affect the pay-off associated with the choice of any given mating tactic. State variables can include physiological states (e.g., energy levels: Lucas and Howard 1995; or sperm storage levels: Harris and Lucas 2002), or some morphological states such as size (Skubic *et al.* 2004).

Dynamic optimization also considers the effect of time horizons on the pay-off to any given mating tactic. For example, a male near the end of his life can "afford" to expend relatively excessive amounts of energy on advertisement or territorial defense because little future reproduction is sacrificed with an excessive expenditure. In contrast, a young male may be selected to be more conservative in his expenditure if this reduced expenditure protects large expected future reproductive benefits (e.g., Lucas and Howard 1995; also see Clark 1994).

The game-theoretic component of a dynamic game acknowledges the role of both frequency- and density-dependent pay-offs on the evolution of behavior (Houston and McNamara 1987, Lucas and Howard 1995). Indeed, a critical component of the evolution of alternative mating tactics is the fact that the pay-off to any given tactic (e.g., territoriality) is affected by the frequency (and often density) of tactics played by other members of the population (Dawkins 1980, Maynard Smith 1982, Parker 1984). The ability to combine complex state-dependent and temporal-dependent pay-offs with frequency- and density-dependent pay-offs makes for an extremely powerful theoretical approach to mating systems.

Two additional points are worth mentioning. One is that while genetic polymorphisms are explicitly considered when investigating alternative strategies using a Mendelian approach, genetic polymorphism is also implicit when studying mating tactics that are under developmental or behavioral control (Grafen 1984). That is, for any trait to be of evolutionary interest, genetic variation underlying trait differences must be involved. The phenotype influenced by genetic differences may be influenced by environmental conditions experienced during ontogeny (reflecting a genotype × environmental interaction) or may be sufficiently plastic to change instantaneously with changing social conditions (reflecting a short-term behavioral response). In nature, selection favors the best genetic option of the ones available. In modeling, one solves for the optimal solution and implicitly assumes that the genetic variation in the population was sufficient eventually to settle on this solution. Strictly speaking, a dynamic game begins with a monomorphic population with a single state- and time-dependent tactic into which competing strategies are introduced, and the tactic that remains is one that cannot be invaded by a mutant playing any alternative tactic. As Mayr (1983) and Grafen (1984) noted some time ago, our "black boxing" of genetics using optimization techniques (Grafen's "phenotypic gambit") may not be appropriate in all cases, but it has proved to be a surprisingly reasonable approach in most studies that employ it.

The second point is that not all mating systems can be easily characterized as solely under genetic, developmental, or behavioral control (see Taborsky 1998, 2001). For example, side-blotched lizards typically exhibit three different, genetically determined strategies: territorial male; nonterritorial, female-guarding male; and a female-mimic male (Sinervo and Lively 1996). However, the mate-guarding male can alternatively develop into a female mimic depending on the availability of females (Sinervo *et al.* 2001). In Atlantic salmon, rapidly growing young males may become sexually mature early in life. These males, known as "parr," remain in fresh water rather than migrating out to sea to continue development. Parr are a fraction of the size of anadromous males and employ a sneak alternative tactic to gain fertilization success. However, because this species is iteroparous, parr may subsequently migrate out to sea and return as territorial anadromous males (see review by Fleming and Reynolds 2004). Similarly, plumage patterns in the ruff are heritable (Lank *et al.* 1995, 1999). Dark-collared birds defend small mating territories on a lek; white-collared males can act as sneaker males when they dart onto a territory and mate with females, but they can also court females that arrive on a lek. Hybrid models are required in all three of these examples. For example, we could treat the ruff system as a game played within a game: white-collared birds play a dynamic game against other white-collared birds and choose their mating tactic accordingly. However, this game is nested within a genetic game played by white-collared birds against dark-collared birds. Two-level dynamic games have been described by Alonzo and Warner (2000a, b). These may provide some insight into the design of hybrid models.

Gross and Repka (1998) provide an analytical solution to the evolution of condition-dependent, developmental switching rules where tactics do not breed true. This latter analytical method is preferable to the multilevel dynamic games described by Alonzo and Warner (2000a, b) because the model is easier to interpret, but the dynamic game approach is the only complete solution available for complex systems with behaviorally regulated ARTs (see Section 4.4).

4.3 THE DYNAMIC GAME-THEORY APPROACH

4.3.1 Behaviorally regulated traits

We now narrow our discussion to modeling behaviorally regulated tactics. Some authors have suggested that behavioral regulation of alternative male mating tactics is ubiquitous (e.g., Gross 1996), although there is some debate about the prevalence of this class of mating behavior (e.g., Shuster and Wade 2003). What is clear from the literature is that behaviorally regulated alternative mating tactics are common in many mating systems and probably truly ubiquitous in some. Thus, an analysis of the theoretical aspects of behavioral regulation of mating tactics is highly relevant to our understanding of their evolution.

Our model entails optimal decision-making; that is, in any given time interval, an animal chooses to perform any one of the alternative behavior patterns in its repertoire. The particular behavior chosen has two consequences: an immediate fitness pay-off to the individual if it reproduces and a change in its future reproductive success. The change in future reproductive success is caused by changes in physiological state (such as a reduction in energy level, size, or sperm stores) and by changes in mortality risk (for example, through predation or starvation) incurred when expressing a chosen behavior. These future pay-offs should in turn affect the current decision. Thus, each decision has cascading effects into the future by affecting physiological state and mortality risk, and these cascading effects will, in turn, affect choice between alternative decisions at any given time. This pattern of temporal cascading is dynamic optimization (Houston and McNamara 1999, Clark and Mangel 2000).

Ecological conditions will dictate, in part, how far into the future the temporal cascade extends as a factor influencing a decision. For example, if predator density is high or food abundance is low, then the "time horizon" of the cascade's effect will be relatively short. However, time horizons are complex, multidimensional phenomena. Consider a situation in which an animal faces starvation because of low food abundance. The risk of starvation could result from three different thresholds (see discussion of the "lazy L" in Stephens and Krebs 1986): (1) a constant, immediate risk of starvation if energy stores fall below some threshold; (2) a daily threshold if the animal requires energy stores to survive a period when feeding is not possible (e.g., at night for a diurnal species); and (3) a seasonal time horizon if sufficient stored reserves are required to survive for long periods such as winter. Each of these thresholds could simultaneously influence any given decision, and the relative importance of each threshold varies with time of day and season. In addition, the animal's decision is also influenced by its current energetic state and a host of other conditions. At first glance, such complexity seems too great to handle, but the beauty of dynamic optimization is that dynamic programming makes it fairly easy to model multidimensional thresholds.

In addition to ecological conditions affecting decisions, the presence of conspecifics competing for the same food or mates means that the decisions of others will influence an individual's choice of behavior. This is where the game part of dynamic game theory is important in that the pay-offs to any decision will, in part, be affected by the frequency or density of occurrence of the behavior in the population.

In sum, dynamic games involve a cascading feedback between an individual's behavioral choices and its physiological state, and pay-offs to the decisions are affected by frequency- and density-dependent trade-offs. The algorithm used to find the evolutionarily stable state (ESS) has two parts (see Houston and McNamara 1987): a backward iteration (or dynamic program) and a forward iteration (or simulation). In our example, 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 (Houston and McNamara 1999, Clark and Mangel 2000) to find the best strategy that a single male should play against this population. We then use a simulation to determine the composition of a chorus composed entirely of these mutants. This two-part process is repeated until the best mutant tactic is identical with the tactic shown by the rest of the population. This tactic is the ESS.

4.3.2 Empirical issues

To illustrate the utility of the dynamic game approach to investigating alternative mating tactics, we will concentrate on caller/satellite interactions in anurans. Callers expend energy advertising for females, while satellites act as reproductive parasites by intercepting females attracted to calling males. Given space constraints, we will describe the model in general terms here. Details can be found in Lucas and Howard (1995; also see Lucas *et al.* 1996) and in Appendix to this chapter (Section 4.5).

Caller/satellite interactions include all of the features mentioned above for a dynamic game: males can switch between each tactic, sometimes within an evening (Perrill *et al.* 1978); calling is energetically expensive (Taigen and Wells 1985, Grafe *et al.* 1992, Cherry 1993) and involves a risk of predation (Howard 1978, Ryan *et al.* 1981); and the pay-offs to each tactic are frequency-dependent (Arak 1988) and most likely density-dependent (Ryan *et al.* 1981, Dyson *et al.* 1992, Wagner and Sullivan 1992). To model caller/satellite tactics using dynamic game theory requires information on five general properties: an individual's physiological state, prevailing environmental conditions, frequency- and density-dependent pay-offs to each tactic, and time constraints. All five properties are best considered simultaneously rather than singly because they interact with each other. Below, we discuss the relevance of each property and their relationships to each other. We will make several points based on results derived from the Lucas and Howard (1995) model. We assume that males have a repertoire of four behavior patterns: calling, acting as a satellite, leaving the chorus to forage, and leaving the chorus to hide in a refuge. We model a population in which the breeding season is at most 50 days long, contains 1000 males (summed over all age classes) on the first day of the breeding season, and consists of males whose energetic stores can be arbitrarily divided into 30 intervals. For simplicity, we assume that there are two classes of males (1-year-olds and 2-year-olds). Although data on the effect of male age on mating success are rarely reported for anurans and morphological correlates of age such as body size may only distinguish first-time breeders from older males (e.g., Halliday and Verrell 1988), we assume that calling 1-year-old males attract only 70% as many females as calling 2-year-old males (e.g., Howard 1981). Initially, we assume that the reproductive rate of satellites of both ages is 50% of the reproductive rate of 2-year-old males (e.g., Miyamoto and Cane 1980, Sullivan 1982, Tejedo 1992). Overwinter survival for 1-year-old males is assumed to be dependent on the energy reserves of the male at the end of the season, with a maximum survival probability of 0.75 (e.g., Clarke 1977, Howard 1984, Caldwell 1987). The values used are roughly based on empirical estimates from several anuran species but are certainly not meant to be representative of all anurans (Lucas and Howard 1995).

(1) PHYSIOLOGICAL STATE

Continuous chorus attendance by male anurans is usually limited to a few consecutive nights (e.g., Dyson *et al.* 1992, Murphy 1994a, Given 2002) with male condition declining with longer chorus tenure (Murphy 1994b, Judge and Brooks 2001, Given 2002). Murphy (1994b) and Marler and Ryan (1996) showed experimentally that chorus tenure is significantly influenced by energetic state (but see Green 1990, Judge and Brooks 2001). Bevier (1997) has shown that glycogen levels in trunk muscle tend to decrease more rapidly in species where males have high calling rates. Because satellite males do not call, there should be significant energetic differences between caller and satellite mating tactics. The bulk of evidence points to energetics being an important component in chorus attendance, but few studies provide quantitative information on this point. Obviously, we need to know the energetic consequences of each decision. However, even a thorough knowledge of the dynamics of a male's physiological state will not give us a complete understanding of the evolution of alternative mating tactics, in part because environmental conditions should also affect the evolution of these traits.

(2) ENVIRONMENTAL CONDITIONS

Environmental conditions can influence behavioral decisions in several ways. We will illustrate this point with an example from our original model (Lucas and Howard 1995). We consider two environmental conditions: the number of days remaining in the breeding season and the degree to which climatic conditions are favorable for breeding. For the latter, we assume that female arrival rate to a chorus is partly a function of weather (e.g., rain).

Our model generates the following predictions. When environmental conditions are often conducive for high female-arrival rate, chorus formation will be promoted. Under these conditions, 2-year-old males with high energy stores should stay in the chorus and call and 2-year-old males with low energy stores should leave the chorus and forage (Figure 4.1A). However, the threshold level at which 2-year-old males leave and forage declines as the season progresses. Thus, a male's energy stores should influence whether it enters a chorus, but the effect of energetic state on a male's mating behavior is most critical early in the season when the time horizon for future mating opportunities is relatively long.

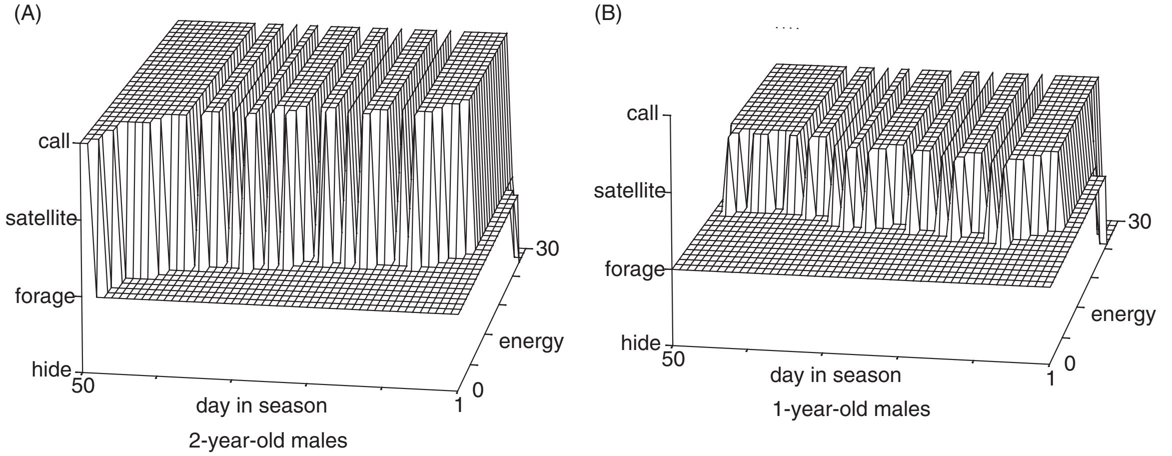

Figure 4.1 Decision matrix for males as a function of day in season and energetic stores. This simulation assumes that most days are conducive for chorus formation ($P_{\text{goodday}} = 0.8$), that mating success of satellites is 50% of the success of 2-year-old callers, and that 1-year-old males get 70% of the mating opportunities of 2-year-old males if they call. The cost of calling is -2.5 (1.4 energy units per night). Note that (A) 2-year-old males call if they have high energy stores; (B) 1-year-old males choose to become satellites if they have high energy stores; the threshold energy at which 2-year-old males call decreases as the season progresses; and throughout the middle of the season all males are predicted to leave the chorus periodically in order to forage. Note that the lower right corner of this figure represents the beginning of the breeding season (day 1) and represents males with the lowest energy reserves (0).

Predictions differ for 1-year-old males: under the same conditions, 1-year-old males are expected to use satellite tactics throughout the breeding season (Figure 4.1B). The exclusive use of the satellite tactic by younger males is caused by several factors. Satellite tactics are assumed to require less energy than calling, and extended periods of environmentally favorable days for chorusing puts a premium on energetic efficiency. Furthermore, the pay-offs for calling differ: 1-year-old males attract fewer females by calling than 2-year-old males do. The net result is that 1-year-old males should weigh future reproductive success more strongly than 2-year-old males, and they should therefore choose a more conservative tactic than 2-year-olds. The more conservative strategy chosen by 1-year-olds causes the mass threshold for leaving the lek to increase as the season progresses – a trend opposite to that seen in 2-year-olds. Thus 1-year-old males in marginal condition at the end of the season should avoid the costs of entering the chorus; whereas 2-year-old males in marginal condition should accept these costs because these older males have less to lose if they die.

Regardless of age, males are predicted to move in and out of the chorus within a period of 4 to 7 days. Males are predicted to leave choruses because, under our assumptions, they will starve if they call continuously for more than 10 days, even if they begin with full fat stores. However, males are predicted to leave choruses well before they face these energetic constraints. Males leave earlier than expected based on energetic considerations because frequency- and density-dependent pay-offs should contribute to the coherence of a chorus.

(3 AND 4) FREQUENCY- AND DENSITY-DEPENDENCE

Our model suggests that low-energy-state males are forced to leave every few days because they need to avoid starvation by foraging. The loss of these males from the chorus, in turn, potentially reduces the value of chorus attendance by males with relatively high energy states. The high-energy-state males leave because we have assumed that predation risk is both frequency (i.e., lower for satellites) and density dependent, and that female arrival rate is chorus-size dependent. The net result is what appears to be a pulsing chorus because males move in and out of the chorus without any change in environmental conditions. Note that the departure of low-energy-state males reduces the tendency for any other males to enter the chorus. This pulsing will be reinforced by an entrainment of energy states of males in the population because many males will be foraging or entering the chorus at the same time, and the modal energy state shown by males in the population will therefore cycle along with the pulsing of the chorus.

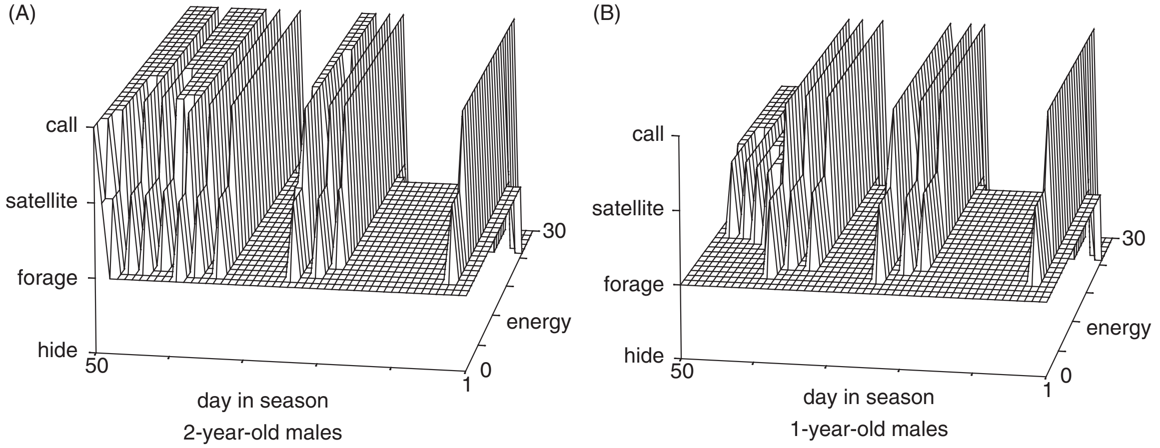

Figure 4.2 Decision matrix for males as a function of day in season and energetic stores. This simulation assumes the same factors listed in Figure 4.1 and additionally assumes that the cost of calling is increased 40% over the cost assumed in Figure 4.1. (A) Note that 2-year-old males call if they have high energy stores, convert to being satellites at intermediate energy stores, and leave the chorus to forage at low energy stores. (B) The same is true of 1-year-old males, except that 1-year-old males do not call at the end of the season. Also, all males spend more days during the season foraging thus limiting the total number of days the chorus is active.

Numerous other factors could also influence frequency- or density-dependent trade-offs when pay-offs are measured in terms of increased mating success and reduced predation risk. For example, the pay-off to utilizing either the calling tactic or the satellite tactic should depend on the percentage of males in the chorus that are currently using each tactic (which should, in turn, be a function of the age/size distribution of males in a population). The density of calling males should be positively correlated with the arrival rate of females and negatively correlated with the risk of predation each male might experience. However, merely stipulating the sign of these correlations is insufficient; the form of both functions (i.e., linear, accelerating, dampening) can be critical.

The relevance of each factor we have discussed thus far can be demonstrated with the following example. Physiological studies indicate that the cost of calling varies considerably across species (see review in Gerhardt and Huber 2002). For species with a particularly high cost of calling, we predict that chorus attendance should decrease dramatically in 2-year-old males (compare Figure 4.2A with Figure 4.1A). Early in the breeding season, 1-year-old males should enter a chorus as satellite males if they have low energy stores and they should call only if they have high energy stores. In contrast, 1-year-old males should use the satellite tactic exclusively toward the end of the season, even if they have high energy stores (Figure 4.2B). Of course, the use of the satellite tactic by 1-year-old males is only viable if 2-year-old males call. In other words, frequency-dependent trade-offs associated with the caller/satellite decision determine critical components of chorus dynamics.

The above predictions assumed that favorable environmental conditions prevail during the breeding season. In this case, energetic constraints will limit chorus attendance, and density- and frequency-dependent pay-offs will dictate how the population responds to these energetic constraints. However, unfavorable environmental conditions are predicted to eliminate both of these effects. If rain is less frequent during the breeding season, we predict that 2-year-old males should call on the few days that rain does occur (data not shown). Because a succession of rainy days should be uncommon, 2-year-old males never have the option of remaining in a chorus for periods long enough to jeopardize their energy stores. Thus, infrequent rains effectively shorten the time horizon associated with the energetic cost of chorus attendance. Males will only chorus for short intervals of time and will then have sufficient time to recoup energetic expenditures before it rains again. No pulsing of the chorus is expected as seen under more favorable and continuous breeding conditions.

When conditions favorable for breeding are rare during the season, energetic constraints should also be less relevant for 1-year-old males. These males should maximize their chances of mating on favorable days by calling rather than using the satellite tactic. The 1-year-old males should only adopt the satellite tactic early in the season, and only if they have a long breeding future.

Clearly, to understand the dynamics of chorus activity, we need to know the energetic consequences of each alternative behavior, but there are a host of frequency- and density-dependent factors that could also exert effects. In particular, these factors should affect the cohesiveness of a chorus and thereby override energetic effects. Finally, all of these effects are moderated by environmental conditions.

(5) TIME CONSTRAINTS

The last property needed to parameterize dynamic games is time constraints. As explained above, energetic constraints should have less effect on 2-year-old males than 1-year-old males as the breeding season progresses, because mating opportunities end with the current year for 2-year-old males; in contrast, 1-year-old males may survive for another year. If 1-year-old males survive the subsequent winter, prospects for mating success will be high in their next breeding season, as then they will be 2 years old. Thus, 1-year-old males have a longer time horizon than 2-year-old males. This should reduce the correlation between energetic thresholds and time of season and should cause 1-year-olds to choose an energetically conservative strategy all year long (see Figure 4.1). More generally, the reproductive consequences of most mating behavior patterns are likely to be affected by a variety of limited time horizons. A complete understanding of these time horizons is important in our characterization of behaviorally mediated mating tactics.

4.3.3 Incorporating all five factors: an example

Counterintuitive predictions can result from our model under specific parameter levels of the five factors we have outlined. In general, calling males and satellite males have an uneasy truce. Males call to attract females and the presence of callers makes the satellite tactic viable. If the cost of chorus attendance is sufficiently high for 1-year-old males, they should only enter a chorus as satellites; however, if callers suffer a significant reduction in mating success because of the presence of many satellite males and if the risk of predation is also high, then 2-year-old males that would otherwise call should not enter the chorus at all (Figure 4.3A). The consequence is no chorusing for extended periods of time. Callers stay away because the prospects of obtaining a mate are too low and chances of predation too high; satellite males stay away because there are no callers to parasitize (Figure 4.3B). Importantly, our simulation showed that every male would have a higher fitness if all individuals called in a chorus early in the season; however, this is not an ESS because it can be invaded by a male who plays satellite at least some of the time. Instead, the only ESS is for no one to call until they essentially run out of time in the season. At the end of the season,

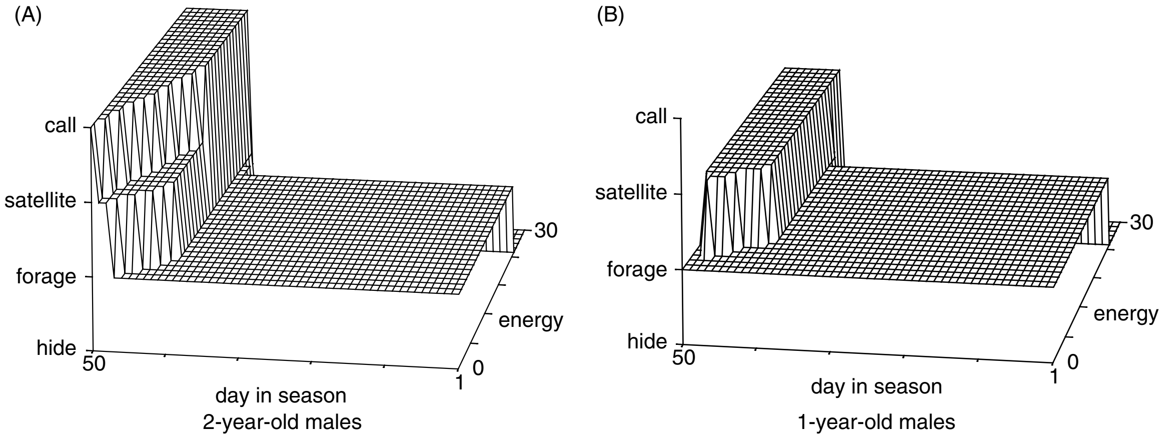

Figure 4.3 Decision matrix for males as a function of day in season and energetic stores. This simulation assumes the same factors listed in Figure 4.1, except that the mating success of satellites is 80% of the success of callers. Note that (A) 2-year-old males change to the satellite tactic if their energy stores are low, but otherwise call; (B) 1-year-old males become satellites if they have high enough energy stores. In addition, the total duration of the chorus is only 9 days.

2-year-old males have no alternative but to enter the chorus because they will not survive to breed again. The presence of 2-year-old males with high energy loads that choose to call provides a viable option for 2-year-old males with low energy stores to act as satellites. In addition, the presence of calling 2-year-old males makes it viable for 1-year-old males to enter the chorus. Whether these males call or use the satellite tactic will depend on the frequency- and density-dependent trade-offs when in competition with calling 2-year-old males. Under the conditions we simulated here, they should always enter as satellites. Thus, the joint effect of time constraints, environmental factors, game aspects, and energetic constraints all dictate the expression of mating behavior patterns in this example.

4.3.4 Graded signals: an extension of the model

Although caller/satellite roles differ qualitatively, alternative mating tactics may also involve quantitative decisions such as the timing of when males display, and these quantitative decisions can be the basis for mating polymorphisms in a population (e.g., Boyko *et al.* 2004). Although these polymorphisms may be more subtle than qualitatively different roles, dynamic game theory can be used to investigate decision-making in these situations and thus increase our appreciation of the evolution of mating systems. Indeed, qualitative and quantitative differences are not mutually exclusive categories of behavior. For example, males exhibiting a qualitatively distinct class of signaling behavior may nonetheless show quantitative variation in the intensity of this signal. Below we extend our original caller/satellite model to illustrate how we can use dynamic game theory to study quantitative signal variation nested within qualitatively different mating tactics.

Starting with Zahavi (1975), research on signal design has focused on the factors that contribute to the evolutionary stability of signals that honestly advertise the quality of a mate (Grafen 1990, Maynard Smith 1991, Johnston and Grafen 1992). The consensus is that for signals shared among nonrelatives, the signal needs to be expensive to produce and the relative fitness consequences of producing an enhanced signal must be greater for low-quality males than for high-quality males. The models assume that females cannot detect male quality directly but can only infer quality from male signals – hence the issue of honesty and the potential for dishonest signaling (i.e., low-quality males providing high-quality signals).

In virtually all mating systems with alternative mating strategies/tactics, some males indicate their quality to females by providing information in their signals. In caller/satellite systems, calling males can vary acoustic properties of their signals such as call amplitude, rate, or duration, and females appear to prefer more exaggerated calls (reviewed by Gerhardt and Huber 2002). We know of no studies that have investigated whether the presence of satellite males affects any of these call properties of calling males.

Given the greater cost of producing a louder, longer, or more frequent call, it is assumed that these call properties can provide honest advertisements of calling-male quality. However, models used to study the evolution of honest signaling have primarily been static game-theory or genetic models (Grafen 1990, Maynard Smith 1991, Johnstone and Grafen 1993, Johnstone 2000, Gintis *et al.* 2001). While game-theoretic models have contributed significantly to our understanding of signal evolution, they leave out a potentially critical component of signal cost. In particular, the fitness consequence of investing energy on mating advertisements may change dynamically for signalers, as we have illustrated above. For example, an energetic expenditure early in a breeding season may have greater fitness consequences than an identical expenditure at the end of a breeding season. How do these dynamic components of a signaling system affect the evolution of the signal?

Proulx *et al.* (2002) showed that game-theoretic models with age structure generate different predictions than static models because young individuals have more to lose from risky signaling than do old individuals. As a result, we expect young individuals to be more conservative than old individuals when signaling; thus, we expect the signals from old individuals to be a more honest representation of quality compared to signals from young males. Although Proulx *et al.* (2002) incorporated age effects in their model, time-dependent changes in state were not explicitly treated. Dynamic games provide a mechanism to do just this and therefore can be used to evaluate the conclusions of Proulx *et al.* (2002) more completely.

To address these issues, we modified our original model to incorporate a graded call signal. We assume that the cost of an exaggerated signal falls under the category of "receiver-independent costs" (Vehrencamp 2000). That is, signaling cost is independent of the target receiver's response, as would be expected if the primary cost of producing a signal is either energetic or a risk of attracting predators. We assume that call exaggeration affects three aspects of a male's reproductive success:

(1) Relative attractiveness to a female. Assume that this is a monotonic increasing function of call investment ("intensity") but with diminishing returns. We simulate this function as

$$\text{RelAttractiveness(intensity)} = 0.4 + (5.21 \times (\text{intensity} - 1)^{0.5})/9. \quad (4.1)$$

(2) Energetic cost of call production. We modeled this relationship as a linear function of intensity following data cited in Gerhardt and Huber (2002):

$$\text{COST(intensity)} = 0.5 + (\text{intensity} - 1)/3. \quad (4.2)$$

(3) Relative risk of predation. We modeled the effect of call intensity on caller predation risk using an accelerating function of intensity:

$$\text{ProbPRED(intensity)} = 0.6112 + (\text{intensity} - 1)^2/9. \quad (4.3)$$

To simplify the analysis, we used four levels of call intensity (1–4). Increasing the number of levels to eight did not alter predictions, however. For all three functions, the coefficients were set such that there was a mean of 1.0 in the effect (attractiveness, energetic cost, or predation risk) for an equal weighting of the four intensity levels. Note that the functions described above are used as multipliers of the background attractiveness, energetic cost, and predation risk used in the original model (see Appendix, Section 4.5).

Results show firstly that the general properties of our original model are not altered if calling males use graded calls. For example, in environments conducive for chorus formation (i.e., probability that the environment is appropriate for a chorus on any given day, $P_{\text{goodday}} = 0.8$), males are expected to show pulses of mating activity punctuated by 1- to 2-day intervals where all males leave the chorus to eat. This pulsing is not shown in drier environments (e.g., $P_{\text{goodday}} = 0.4$). Also, not surprisingly, 1-year-old males will tend to act as satellites, and 2-year-old males should tend to call. The degree to which the satellite tactic is employed will depend on the relative success of satellites compared to callers. These are important results, because they suggest that our original results are robust to minor modifications of the model.

Secondly, our results partially support and extend the conclusions of Proulx *et al.* (2002). The relative shape of the intensity functions will strongly influence the results from the model. Due to space limitations, however, we will not explore this aspect of the model here. Instead, we will use Eqs. (4.1) to (4.3) to illustrate a few points about honest signaling. If mate availability for satellites is only 40% of that for the mean caller and if the environment is favorable on most days ($P_{\text{goodday}} = 0.6$), then both 1-year-old and 2-year-old males call, but calling intensity increases with energy stores on a given day and call intensity changes over the course of the breeding season for both age groups. However, 1-year-old males should tend to call at lower intensities toward the end of the season (Figure 4.4A), whereas 2-year-old males should call at higher intensities at the end of the season (Figure 4.4B). Thus, as Proulx *et al.* (2002) suggest, one could conclude that calls from 2-year-old males appear to be more honest than those from 1-year-old males in that older males' calling intensity is a better reflection of their immediate condition compared to the younger males. However, this conclusion is correct only at the end of the breeding season. At the beginning of the season, a male's calling intensity provides little information to the female about the quality of the calling male.

Our model suggests that the logic of Proulx *et al.* (2002) is sound under certain conditions: at the end of a long season (50 days) in a fairly high-quality environment ($P_{\text{goodday}} = 0.6$). If the conditions are even more conducive for chorus formation ($P_{\text{goodday}} = 0.8$), temporal trends in the intensity of calling by 1-year-old males reverse: they call more intensely at the *end* of the season (Figure 4.4C), as do 2-year-old males (Figure 4.4D). Paradoxically, the season is expected to be shorter for the more favorable conditions because satellite pressure drives callers from the chorus. However, the final stable solution is for all males to call! By eliminating the satellite option, we can show that the "ghost" of satellite pressure is the primary factor generating this pattern. When this happens, males call throughout the season (data not shown). Paradoxical results notwithstanding, the shortened season reduces future reproductive success for 1-year-old males and this in turn causes them to give relatively honest signals toward the end of the breeding season. Thus, the conclusion about age dependency in call honesty is sensitive to assumptions made about environmental conditions and time constraints on future reproductive success. Indeed, a change in a single parameter, such as the quality of climatic conditions, can change qualitative predictions about calling intensity. These results illustrate the value of dynamic game theory. Compared to static game-theory models, these more complex models provide a robust method of calculating future reproductive success and incorporating estimates of future reproductive success into predictions about mating tactics. Of course, this ability to measure future reproductive success comes at a

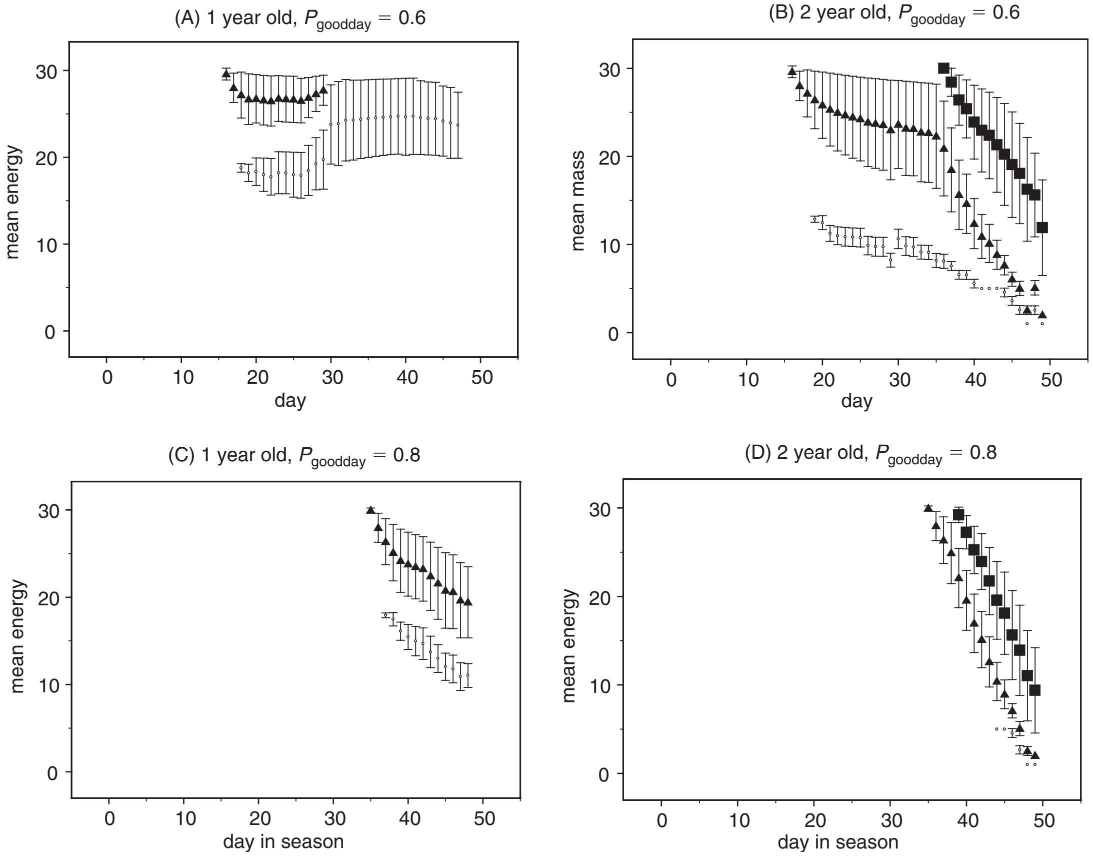

Figure 4.4 Mean predicted energy reserves as a function of time-in-season (day) and call intensity for 1- and 2-year-old males in our modeled population. Note that unlike Figures 4.1 to 4.3, this figure represents the profile of the population that results from the decision matrix, not the decision matrix itself. Panels (A) and (B) represent environments where the probability of a day favorable for chorus formation is 0.6; (C) and (D) represent environments where this probability is 0.8. The different symbols represent different call intensities: small circle = intensity 2, medium triangles = intensity 3, and large boxes = intensity 4. No male is predicted to call at the lowest intensity (1), and no males are predicted to act as satellites under these conditions. If no symbol is plotted for a given day, no chorus is predicted to form on that day (e.g., no chorus forms for the first 34 days in (C) and (D)). Note that 1-year-old males in (A) give less intense calls toward the end of the season, shifting in intensity from a mix of level 2 and 3 intensities around day 20 to only intensity 2 after day 30. The 1-year-old males in (C) tend give more intense calls as the season progresses, with males giving intensity 3 calls over a broader range of body masses toward the end of the season. The latter trend is shown by 2-year-old males for both environments ((B) and (D)). Also, on any given day, low-energy males always give less intense calls than high-energy males if more than one intensity is produced.

cost: the empirical description of a mating system needs to incorporate all five of the factors we listed above.

Dynamic games provide a mechanism for understanding the effect of each of the five critical properties discussed in this chapter. This point is underscored by the limited results we have shown here in our model of graded signals. We assumed that females prefer 2-year-old males, but that male reproductive success is also a function of calling intensity. Should intensity honestly indicate male quality? The answer is yes, but only under limited circumstances. Our results provide evidence that only 2-year-old males should call at maximal intensity. Thus, females should be able to distinguish at least a subset of the highest-quality (older) males from lower-quality (young) males. However, our model assumes that females do not discriminate between males of different energetic states within an age class. Nonetheless, energetic state is predicted to have a profound effect on calling intensity because a male's energetic state will affect his future reproductive success. As a result, variation in calling intensities based on energetic state can blur the distinction between calling properties of high- and low-quality males. The point is that factors such as genetics or parasite load that are relevant to a female in her choice of males may be masked by variation in other factors such as energy stores that reflect stochastic events in an organism's life (see Stephens and Krebs 1986). Models such as the ones we have described here provide us an important tool for understanding the dynamics of these decisions.

4.4 HOW DETAILED SHOULD A MODEL BE?

As in our earlier papers, our goal here is to aid researchers in prioritizing data collection by providing insights on the type of data required to analyze alternative mating tactics. As we have discussed above, alternative mating tactics are complex phenomena in that at least five general factors are involved in their evolution (an individual's physiological state, prevailing environmental conditions, frequency- and density-dependent pay-offs to each tactic, and time constraints). Such interplay between theoretical models and empiricism begs the following philosophical question: should we construct complex models of behavior that push the limits of our ability to collect data, or should we construct simple-models of behavior? We suggest that both approaches are necessary (also see Hilborn and Mangel 1997).

From our perspective, simple models perform a function different from that of more complex models. For example, the hawk/dove game (Maynard Smith 1982) revolutionized the study of behavior by introducing the concept of frequency-dependent pay-offs. This is a perfect example of a simple model that caused us to think about behavior in a new way.

A number of models of the evolution of mating behavior follow this pattern. State-independent game theoretic models provide a single-focus view of these systems. Examples include Waltz (1982) and Arak (1988), who evaluated caller/satellite decisions based on the relative attractiveness of nearby males. More complex, three-player games have also been described. Hamilton and Dill (2002) considered a game with three male strategies (resource owner, satellite, and floater), whereas Hugie and Lank (1997) modeled lekking in ruffs where they considered two male strategies (satellite and territorial males) playing against one another and against females. Hugie and Lank (1997) showed that female choice may constrain all territorial males to have satellites, despite the fact that this reduces reproductive success of the territorial males. This result is analogous to our description of systems where the "ghost" of satellite parasites should keep males away from the chorus, despite the fact that their reproductive success would be higher if they did enter the chorus to call. Gross and Repka (1998) published a very different game-theory model that showed that condition-dependent choice of alternative mating tactics could be stable without equal fitness of the alternative mating morphs if there is partial inheritance of behavior (i.e., male morph α produces some fraction, $p < 1$, of α offspring).

These models have proved to be important in helping us understand specific components of mating systems. However they are, by definition, incomplete, and we cannot know whether their predictions are robust unless a more complex model is developed. Brodin (2000) and Pravosudov and Lucas (2001) provide an example of problems that can arise from models that are too sketchy in their depiction of behavior.

As our caller/satellite dynamic game illustrates, complex models give us some insight into the subtle and sometimes counterintuitive outcomes that can result from the interactions between a myriad of factors that regulate behavior. Indeed, only complex models can give us a way to put this myriad of factors into focus. But what level of complexity is sufficient? Dynamic programs that ignore frequency-dependent pay-offs can offer a partial solution where aspects of games played between males (or between males and females) are simply fixed. Examples of this approach are Fraizer's (1997) analysis of alternative mating tactics in digger wasps and Skubic *et al.*'s (2004) model of reproductive parasitism by subordinate helpers in a cooperatively breeding cichlid fish. Harris and Lucas (2002) showed that a dynamic program of sperm competition was broadly compatible with the game-theoretical models of Parker (1990), but revealed implicit assumptions about environmental factors that could invalidate predictions from the game-theoretical models when the assumptions are not met.

Dynamic games take this complexity one step further. But even with dynamic games, the level of complexity varies between models. In this chapter, we describe dynamic games played between males. A model derived from our previous work (Lucas *et al.* 1996) by McCauley *et al.* (2000) showed that broadly similar predictions could be generated with a slightly scaled-down version of our model. McCauley *et al.* (2000) argue that we do not need such a complex model. The problem is that this statement is meaningless without the one-to-one comparison between models. Even these models ignore multilevel games, which are certainly possible in the evolution of ARTs when female choice affects the pay-offs to males choosing among alternative reproductive tactics, but where the frequency of male tactics in turn affects the pay-offs to females in their choice of reproductive behavior. These multilevel games are described by Alonzo and Warner (2000b, c). Indeed, Alonzo and Warner (2000b) showed that only their most complex multilevel dynamic game explained observed relationships in a game where female Mediterranean wrasses choose spawning behavior, sneaker males choose when to join a nest, and nesting males choose if and when to desert a nest. Of course, complex models may be so complicated that it is difficult to ensure that they are correct. Grafen's (1990) classic model of honest signaling is a case in point (Siller 1998).

Nonetheless, the point we are trying to make in this chapter is that details matter in developing a sound predictive basis for the evolution of behavior. This is particularly true of behavior patterns as complex as alternative mating tactics. We have discussed the fact that the five general properties of behaviorally regulated alternative mating tactics have not been simultaneously incorporated into any study to our knowledge. We hope this short review has given students of mating behavior a good reason to expand their studies to include this broader view of their systems.

4.5 APPENDIX: THE MODEL

This Appendix is largely derived from Lucas and Howard (1995). The original model assumed that calling males had only one option when they enter a chorus, to call at a fixed intensity. We provide one important extension of the original model to allow for graded call intensities.

4.5.1 The original model

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

Males are assumed to choose among four different behavior patterns: call, satellite, forage, or hide in a predator-safe refuge. The latter two 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 behavior patterns is assumed to be based on lifetime mating success. Male mating success is assumed to be a function of (1) the mating tactic chosen by a male, (2) the degree of competition between males, (3) male age, and (4) 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 the size and composition of the chorus. We simplify male age to allow for two age categories, 1-year-old males (males in their first year after sexual maturation) and 2-year-old 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 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 find the best strategy (i.e., the one that maximizes lifetime mating success) a single male should play against this population using stochastic dynamic programming (Houston and McNamara 1999, Clark and Mangel 2000). 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 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 (ESS: Parker 1984; or more specifically, the Nash equilibrium); that is, the strategy that when played by the entire population cannot be invaded by a single mutant playing some alternative strategy.

It usually takes about five to ten iterations for the algorithm to find the ESS, when one exists. However, there are conditions where no ESS is found (see Houston and

McNamara 1987, Lucas *et al.* 1996). In these cases, we present the results of the model after 50 iterations. An alternative approach for unstable models is to allow for partial "invasion" of the mutant strategy into the background population, instead of having the mutant completely replace the background population (McNamara *et al.* 1997; see Boyko *et al.* 2004 for an example). We have found that the solution generated in this manner is nearly identical to the solutions generated from our model when it is unstable because the instability is generated from only a few unstable matrix elements (i.e., combinations of time, state, and environment). We therefore retain the simpler algorithm used in our original paper.

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

SURVIVORSHIP

Starvation rate on any night during the breeding season is taken as a function of the level of energetic reserves and is modeled using an incomplete beta function (note: throughout this appendix, square brackets indicate that the variable is a function of the bracketed terms):

$$\mu_{st}[e] = 1 - I_e[a_e, b_e], \tag{4.4}$$

where $I_e[a_e, b_e]$ = 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 0 (at $e = 0$) to 1 (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 it has the biological realism of finite tails (see Figure 1 in Lucas and Howard 1995).

To run the dynamic program, energetic state and time are divided into discrete intervals. Time is broken into intervals of 1 day. We divided 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 0 to 30), then $\Delta\varepsilon_i \pm \sigma_{\varepsilon_i}$ 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 $\sigma^2 = 2.86$ (note: this is relevant only for the forward iteration).

We assume that overwinter mortality (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 (e):

$$\mu_{\mathrm{ow}}[e] = 1 - I_e[a_{\mathrm{w}}, b_{\mathrm{w}}] \times \gamma_{\mathrm{ow}} \tag{4.5}$$

where γ_{ow} = maximum overwinter survivorship.

Predation rate in a chorus is assumed to vary as a function of chorus size and satellite frequency:

$$\mu_{\mathrm{call}}[\mathrm{date, eq}] = \frac{\beta_{\mathrm{p}} \times (1 - \mathrm{C}[\mathrm{date, eq}])}{1 + \beta_{\mathrm{s}} \times \frac{\mathrm{S}[\mathrm{date, eq}]}{\mathrm{C}[\mathrm{date, eq}]}} \tag{4.6}$$

where β_{p} = maximum probability of a predation event in a caller's territory and date = number of days since the breeding season started. This relationship assumes that predators locate callers, either acoustically or using movement cues, and thus primarily cue on signals emitted by the caller (e.g., Howard 1978, Ryan *et al.* 1981, Perrill and Magier 1988). C [date, eq] is the relative number of calling males on any given day of the breeding season, taken as a fraction of the maximal possible number of males (i.e., the number of males with 100% survival rate), assuming environmental quality "*eq*" (see below). Thus, C [date, eq] reflects both a reduction in chorus size caused by mortality and the proportion of males in the chorus that are calling. Similarly, S [date, eq] is the relative number of satellites in a chorus. The numerator in Eq. (4.6) is the probability of a predation event in a calling male's territory. This is assumed to be a linear function of chorus size. The denominator accounts for the fact that satellites can "share" the risk of predation. Here β_{s} is the risk to a satellite of being killed relative to the risk to a caller. We assume that $\beta_{\mathrm{s}} < 1$. The denominator, therefore, is the effective number of individuals that can be preyed upon 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 on the territory is taken as a fraction of the risk to callers:

$$\mu_{\mathrm{sat}}[\mathrm{date, eq}] = \beta_{\mathrm{s}} \times \mu_{\mathrm{call}}[\mathrm{date, eq}]. \tag{4.7}$$

We assume that predation rates on foragers (μ_{forage}) and on males hiding in a refuge (μ_{hide}) are lower than those on 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 expected future reproductive success. Current mating success, which is nonzero for only 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. This part of the model would have to be altered to include the seasonally adjusted value of a mating in species where the size and survivorship of clutches varies seasonally (e.g., Morin *et al.* 1990). 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 pay-off 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 and decreases thereafter and is modeled using concatenated incomplete beta functions of day in season, "date" (see Figure 1 in Lucas and Howard 1995):

$$\Phi[\text{date}] = \begin{cases} I_{\tau 1}[a_\sigma, b_\sigma] & \text{if date} < T_{\max}/2 \\ I_{\tau 2}[a_\sigma, b_\sigma] & \text{otherwise} \end{cases} \tag{4.8}$$

where $\tau 1 = 2 \times \text{date}/T_{\max}$,
$\tau 2 = 2 \times (1 - \text{date}/T_{\max})$,
a_σ,b_σ = arguments of incomplete beta function,
$T_{\max}$ = last possible date that females could arrive.

In many species, female arrival rates are correlated with environmental variables such as rainfall or temperature, with females typically arriving on warm, rainy evenings (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 a single variable representing environmental quality ("eq"), and assume that female arrival rate is a linear function of environmental quality:

$$\rho[\text{eq}] = \begin{cases} 1-\text{eq}/4 & \text{if eq} \leq 4 \\ 1 & \text{otherwise} \end{cases} \tag{4.9}$$

and eq ranges from 0 (highest quality) to 4 (lowest quality). We assume that eq increments by $+1$ (when eq < 4 and by 0 otherwise) with some fixed probability, $1-P_{\text{goodday}}$, on each day of the breeding season, and reverts to eq $= 0$ with probability P_{goodday}. This is analogous to rain (i.e., a "good" day) immediately increasing the availability of females and to female arrival rate decreasing with the number of days since the last rain. However, "rain" (when eq $= 0$) 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 eq); 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:

$$\xi[\text{date, eq}] = \gamma\xi 1 \times (C[\text{date, eq}] \times 2 + \gamma\xi 2 \times C[\text{date, eq}]^2) \tag{4.10}$$

where $\gamma\xi 1$ = maximum female arrival rate; $\gamma\xi 2$ = constant. If $\gamma\xi 2$ is positive, this function is accelerating (concave up), and if it is negative, the function is decelerating (concave down) (see Figure 2A in Lucas and Howard 1995). 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 into an average caller's territory is

$$F[\text{date, eq}] = \xi[\text{date, eq}] \times \rho[\text{eq}] \times \Phi[\text{date}]. \tag{4.11}$$

This is the average female arrival rate across all territories. However, 1-year-old 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 1-year-old males "attract" fewer females into their territories than 2-year-old males and subsume any type of competition for mates into this age effect. The age difference can be accounted for as follows:

Assuming that any given 1-year-old male is able to attract some fraction ($\gamma 1$) of the number of females a 2-year-old male will attract, and assuming that $p1[\text{date}]$ is the proportion of callers that are 1-year-old males, then 2-year-old males will attract females at a rate

$$v_2[\text{date, eq}] = \frac{F[\text{date, eq}]}{1 - \rho_1[\text{date}](1 - \gamma_1)} \tag{4.12}$$

and 1-year-old males will attract females at the following rate:

$$v_1[\text{date, eq}] = v_2[\text{date, eq}] \times \gamma 1. \tag{4.13}$$

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:

$$Ms_{\text{call}}[\text{age, date, eq}] = \frac{V_{\text{age}}[\text{date, eq}]}{1 + \gamma_{\text{sat}} \times \frac{S[\text{date, eq}]}{C[\text{date, eq}]}} \tag{4.14}$$

where γ_{sat} = 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 is assumed to be age independent:

$$Ms_{\text{sat}}[\text{age, date, eq}] = \frac{F[\text{date, eq}] \times \gamma_{\text{sat}}}{1 + \gamma_{\text{sat}} \times \frac{S[\text{date, eq}]}{C[\text{date, eq}]}}. \tag{4.15}$$

The current mating success of foraging males and hiding males is zero:

$$Ms_{\text{forage}}[\text{age, date, eq}] = \text{Ms}_{\text{hide}}[\text{age, date, eq}] = 0. \tag{4.16}$$

TOTAL LIFETIME REPRODUCTIVE SUCCESS

The total reproductive success of a male equals current mating success plus expected future reproductive success:

$$\begin{aligned}
&Po_{\text{behav}}[\text{age}, \text{date}, \text{eq}, \varepsilon] \\
&= Ms_{\text{behav}}[\text{age}, \text{date}, \text{eq}] + (1 - \mu_{\text{st}}[\varepsilon]) \\
&\quad \times (1 - \mu_{\text{behav}}[\text{date, eq}]) \times \{P_{\text{goodday}} \times \{P_c \\
&\quad \times \left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behave}} \times PO^*[\text{age, date} \right. \\
&\quad \left. + 1, \text{eq} = 0, \varepsilon + \Delta\varepsilon] \right\} + (1 - P_c) \\
&\quad \times \left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behave}} \times PO^*[\text{age}, T_{\max} + 1, \text{eq} = 0, \varepsilon + \Delta\varepsilon] \right\} \} \\
&\quad + (1 - P_{\text{goodday}}) \times \{P_c \times \left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behave}} \right. \\
&\quad \left. \times PO^*[\text{age}, \text{date} + 1, \text{eq} + 1, \varepsilon + \Delta\varepsilon] \right\} \\
&\quad + (1 - P_c) \times \left\{ \sum_{\Delta\varepsilon=-30}^{30} P_{\Delta\varepsilon|\text{behave}} \right. \\
&\quad \left. \times PO^*[\text{age}, T_{\max} + 1, \text{eq} + 1, \varepsilon + \Delta\varepsilon] \right\} \} \}
\end{aligned} \tag{4.17}$$

where

Ms_{behav}[age,date,eq] = current pay-off if the male exhibits behavior "behav",

$\mu_{\text{st}}[\varepsilon]$, μ_{behav}[date] = mortality induced by starvation (a function of energetic state, ε) and mortality induced by predation conditional on behavior "behav" being exhibited,

P_{goodday} = probability of a good day or a day conducive to chorus formation (eq = number of days since the last good day),

P_{c} = probability that the mating season will continue at least another day,

$P_{\Delta\varepsilon|\text{behave}}$ = probability that energetic state is increased by $\Delta\varepsilon$, given that behavior "behav" is exhibited,

PO^* = optimal pay-off 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 eq = 0 (if it is a "good day") or eq + 1 (if it is not a "good day"), and at energy state $\varepsilon + \Delta\varepsilon$.

4.5.2 Graded signals: an extension of the model

We modified the model described above by allowing calling males to vary the intensity of their calls. In effect, this increased the number of mating options each male had because we treated each level of call intensity as a separate mating tactic that could be employed by a male at any time in the breeding season. We assume that the cost of an exaggerated signal falls under the category of "receiver-independent costs" (Vehrencamp 2000). That is, signaling cost is independent of the target receiver's response, as would be expected if the primary cost of producing a signal is either energetic or a risk of attracting predators. We assume that call exaggeration affects three aspects of a male's reproductive success and all of these variables are taken to be a function of call investment, here defined as "intensity" (see Section 4.3.4 for equations):

(1) Relative attractiveness to a female:

RelAttractiveness[intensity].

(2) Relative energetic cost of call production:

COST[intensity].

(3) Relative risk of predation:

ProbPRED[intensity].

The actual levels of male attractiveness are the product of the relative attractiveness and mating success (Eq. 4.14):

$$\begin{aligned}
&\text{MSactual}_{\text{call}}[\text{age, date, eq, intensity}] \\
&\quad = \text{MScall}[\text{age, date, eq}] \times \text{RelAttractiveness}[\text{intensity}].
\end{aligned} \tag{4.18}$$

Similarly the predation risk is the product of the relative risk and caller mortality (4.6):

$$\begin{aligned}
&\mu\text{actual}_{\text{call}}[\text{date, eq, intensity}] \\
&\quad = \mu_{\text{call}}[\text{date, eq}] \times \text{ProbPRED}[\text{intensity}]
\end{aligned} \tag{4.19}$$

and the energetic cost of calling is the sum of the relative cost of calling and the original value used for the cost of calling:

$$\text{COSTactual[intensity]} = \Delta\varepsilon_i \pm \sigma_\varepsilon + \text{COST[intensity]}. \qquad (4.20)$$

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