

Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours

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ABSTRACT

The importance of conflict between the sexes has recently been recognized as a driving force in the evolution of mating systems and reproductive behaviour. Past theory on the evolution of alternative reproductive strategies focused primarily on interactions within a single sex. These interactions can generate frequency- and condition-dependent fitness, which maintain the stable co-existence of alternative reproductive behaviours. We argue that interactions between the sexes (such as female choice and intersexual conflict) are a common but ignored mechanism that will influence the evolution of male alternative reproductive behaviours. Using a modelling approach that links dynamic games, we examine the influence of female choice on the stability and expression of male alternatives. By modelling five different biological scenarios, we show that female choice can suppress the existence of male alternative reproductive behaviours even when frequency- or condition-dependent mechanisms alone would predict their stable co-existence. Furthermore, we find that variation in female choice can lead to the stable co-existence of male alternative reproductive behaviours in the absence of traditional mechanisms known to allow the evolution of reproductive alternatives.

Keywords: alternative reproductive behaviours, life-history theory, multi-player dynamic game models, reproductive strategies, sexual conflict.

INTRODUCTION

The realization that intraspecific variation in behaviour can be adaptive has stimulated extensive research examining the occurrence and underlying mechanisms of alternative reproductive behaviours. These studies have indicated that alternatives in mating behaviour are relatively common and occur in a variety of patterns (e.g. Alcock, 1979; Dawkins, 1980; Gross, 1982, 1984, 1991, 1996; Austad, 1984; Dominey, 1984; Caro and Bateson, 1986; Taborsky, 1994; Henson and Warner, 1997).

It is common for alternatives to exist in the way males gain access to mates or resources. In many species, large males defend territories, while other males adopt non-territorial behaviours (Taborsky, 1994). Variation exists even within this basic pattern. In the bluegill

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sunfish, individual males do not appear to switch between alternative behaviours (Gross, 1982, 1984, 1991). In the bluehead wrasse, each male is non-territorial when small and switches to territorial defence when large (Warner, 1984, 1985; Hoffman *et al.*, 1985). In some frog species, males even switch on a daily basis between alternative behaviours (e.g. Howard, 1984; Arak, 1988).

Ideally, we would like to be able to explain and predict patterns within this variation. For example, we would like to predict whether male alternatives occur in a given situation. If alternatives are predicted, we would also like to know the frequency of male alternatives at equilibrium, whether individual males change behaviour, and the cue that triggers switching between alternatives.

Theoretical studies have focused primarily on determining the mechanisms that allow the stable co-existence of behavioural alternatives and their pattern of expression (e.g. Levene, 1953; Dawkins, 1980; Rubenstein, 1980; Cooper and Kaplan, 1982; Waltz, 1982; Dunbar, 1983; Gross, 1984, 1996; Kaplan and Cooper, 1984; Parker, 1984; Caro and Bateson, 1986; Moore, 1991; Moran, 1992; Charnov, 1993). Many researchers have argued that condition- and frequency-dependent reproductive success are the two main mechanisms that facilitate the stable co-existence of discrete alternatives (Cooper and Kaplan, 1982; Waltz, 1982; Austad, 1984; Dominey, 1984; Gross, 1984, 1996; Kaplan and Cooper, 1984; Parker, 1984; Caro and Bateson, 1986). Frequency-dependence occurs if the fitness of a behaviour depends on the frequency of behaviours adopted by other individuals in the population. For example, the cost of defending a territory may depend on the number of males competing for a given site. Theory predicts that if two reproductive behaviours are negatively frequency-dependent, alternatives can be maintained (Maynard Smith, 1982, 1988), and this has been observed in a variety of systems (e.g. Gross, 1984, 1991).

Condition-dependence may also maintain alternatives in a population (Dawkins, 1980; Eberhard, 1982; Austad, 1984; Gross, 1984, 1996). A behaviour may depend on the size, age or energy reserves of the individual. For example, large individuals may be better fighters and thus more able to secure and defend territories (e.g. Alcock, 1979). Similarly, some behaviours (e.g. sneaking) may be performed more successfully if the individual is small. Past work has clearly demonstrated the importance of these two mechanisms in determining the existence and pattern of male alternatives (e.g. Metcalfe *et al.*, 1989; Gross, 1991). However, our understanding of alternative reproductive behaviours is in no way complete.

Female choice is commonly ignored in studies of the evolution of male alternative reproductive strategies. Both frequency- and condition-dependence focus primarily on interactions between males. Although the existence of conflict between the sexes is now widely recognized as a critical force driving reproductive strategies, the importance of female behaviour in determining the fitness of male alternative reproductive behaviours has been virtually ignored (but see Henson and Warner, 1997; Luttberg, 1997; Maxwell, 1998; Luttberg and Warner, in press). However, a comprehensive theory of alternative reproductive behaviours must include not only interactions within a sex (through frequency- and condition-dependence), but must simultaneously consider interactions between the sexes (Henson and Warner, 1997).

Our goal here is to determine the extent to which female choice can alter basic predictions regarding the pattern and occurrence of male alternatives. After discussing the basic structure of a multi-player dynamic game, we examine a variety of biological scenarios. For each of the five cases, we compare the predicted effect of female choice on male alternative reproductive behaviours with predictions that consider only frequency- or

condition-dependent male fitness. We then explore two cases of male frequency-dependent alternatives that differ in their effect on female fitness. Next, we examine a simple case of condition-dependent male behaviour. We then consider size- and frequency-dependent male alternatives where female reproductive success differs between alternatives. Finally, we consider a case of female condition-dependence. Within each scenario we discuss the situations under which male alternatives are predicted to occur and the degree to which female choice alters basic predictions. Clearly, these models will not exhaust all possible cases. Although we present each scenario in a specific biological context, each model is constructed such that the basic results are more broadly applicable. We focus on demonstrating the general importance of female choice as a mechanism in determining the pattern of expression and occurrence of male alternatives.

AN ALGORITHM FOR DYNAMIC STATE VARIABLE GAMES

Dynamic state variable models (Houston and McNamara, 1988, 1992; Mangel and Clark, 1988; Mangel, 1990a; McNamara and Houston, 1990; Mangel and Ludwig, 1992; Clark and Mangel, 1999) allow one to examine trade-offs between present and future fitness through the use of a state variable (e.g. size or energy reserves) and an iterated fitness equation. A dynamic state variable game includes a backward iteration and a forward simulation (Houston and McNamara, 1987; Mangel and Clark, 1988; Mangel *et al.*, 1994). The model predicts a strategy matrix where one behaviour is optimal for every given state and time combination. The optimal solution matrix is then used in a forward simulation to calculate the frequencies of states and behaviours. These frequencies become parameters in the next optimization round. This is repeated until the optimal solution matrix remains the same, indicating that it is stable against invasion by any other strategy. We use a method proposed by McNamara *et al.* (1997) to find a stable solution, in which the behaviour predicted is actually the probability of adopting one of two behaviour choices. This allows the model to predict a continuous distribution of strategies rather than only a discrete polymorphism.

We extend this basic method to allow interactions between and within the sexes to be considered simultaneously. The models discussed here include dynamic programming equations for males and females. The two fitness equations are linked by the fact that female choice determines male mating success and male mating behaviour creates the choices available to females. To combine the two dynamic programming equations, their fitness functions must be interdependent (Fig. 1). Although this approach was developed to examine interactions between the sexes, it can clearly be extended to address a variety of multi-player game interactions. For further details on the multi-player dynamic game method, see Appendix 1. By considering the two mechanisms proposed to drive the existence of alternative reproductive behaviours, as well as the interactions between the sexes, we can make more comprehensive predictions regarding the existence and pattern of alternatives predicted to occur.

SCENARIO 1: MALE NEGATIVE FREQUENCY-DEPENDENT ALTERNATIVES

To examine the potential importance of female choice on male alternatives, we first consider a very simple static model of female choice and male alternatives. Imagine a species in which males can use courtship sites to attract females. If these sites are not limiting and do not

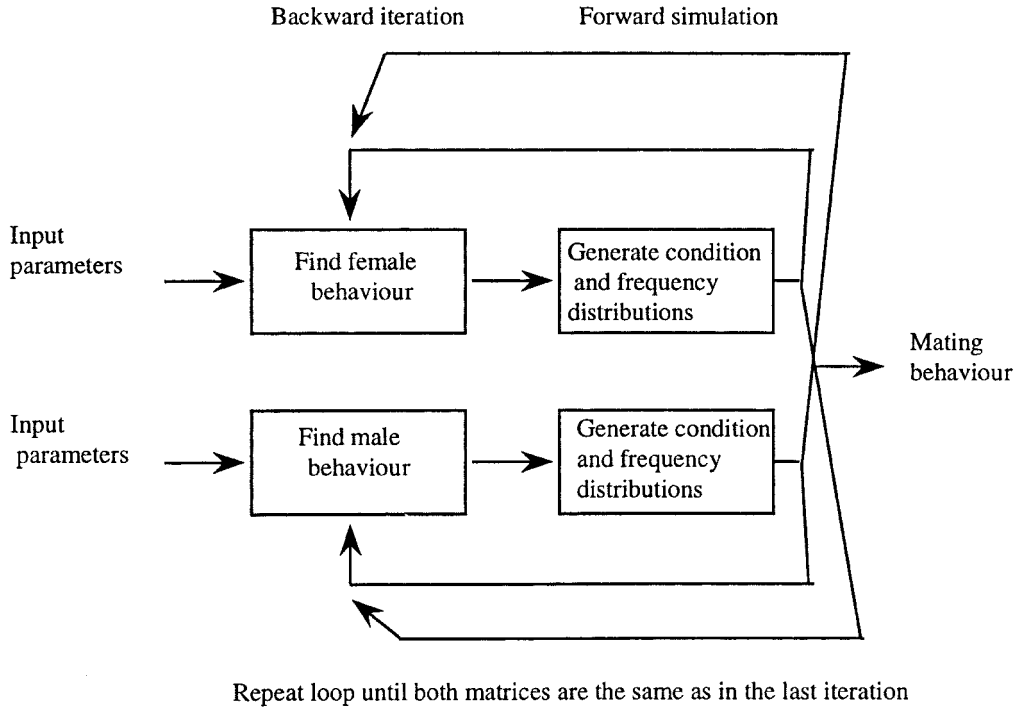


Fig. 1. The modified dynamic programming game for multiple players.

vary in expected reproductive success, males should not compete directly for territories. However, the more males there are displaying from these sites, the less successful each male will be in attracting females. Assume that males can adopt an alternative behaviour that simply entails intercepting passing females. Intercepting males will have higher mating success when most males in the population are displaying on courtship sites, but success will decrease as the number of males intercepting females increases. This type of mating system will cause the fitness of either alternative to be negatively frequency-dependent (Fig. 2). Define the two male behaviours as courting and intercepting. Assume that male success in either behaviour depends only on the relative frequency of male types (f_C and $f_I = 1 - f_C$) and the pattern of female choice (C). The fitness of the alternatives differs only in their immediate mating success. Let F denote the maximum expected male reproductive success. The fitness values of intercepting (V_I) and courting males (V_C) are:

$$\begin{aligned} \text{intercepting males: } V_I &= \alpha / (1 - f_C) (1 - C) \\ \text{courting males: } V_C &= (1/f_C) C \end{aligned} \quad (1.1)$$

And maximum expected male fitness is

$$F = \max\{V_I, V_C\} \quad (1.2)$$

Female preference (C) is a value between 0 and 1, where 0 = complete preference for intercepting males, 0.5 = no preference and 1 = complete preference for courting males. Female preference is predicted by the solution of the female fitness equation. For example,

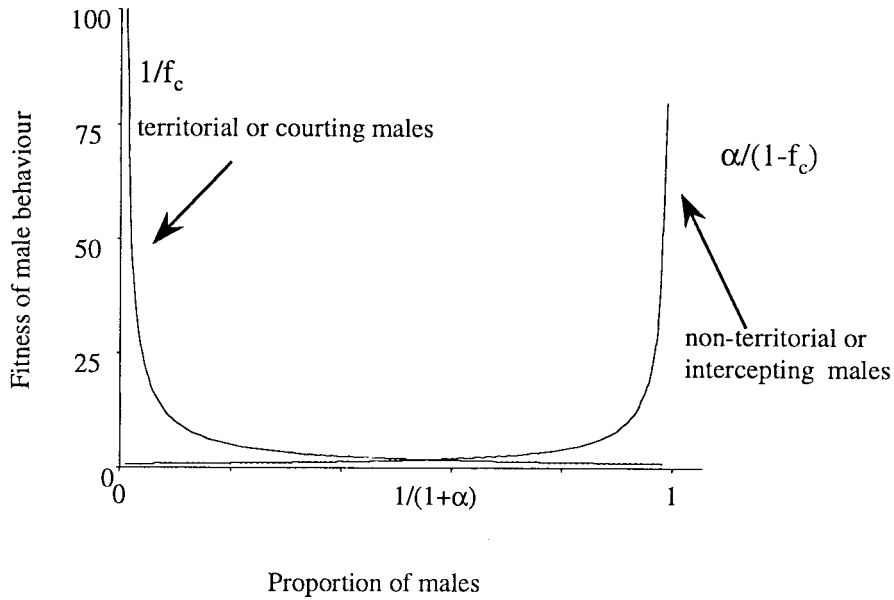


Fig. 2. Negative frequency-dependent fitness of male alternative reproductive behaviours. α represents the degree to which one alternative's overall mating success is less than the other alternative ($0 < \alpha < 1$).

if females have higher fitness mating with an intercepting male, then C will be zero. If the fitness of the two alternatives is equal for females, their preference (C) will be 0.5.

Male alternatives will co-exist when the fitnesses associated with both choices are equal. This will occur when $V_I = V_C$, which implies that

$$f_c = C / [(1 - C)\alpha + C] \quad (1.3)$$

If $C = 0$ (females prefer intercepting males) $f_c = 0$, and if $C = 1$ (females prefer courting males) $f_c = 1$. If females prefer one male alternative, then only that alternative will occur in the population. Male alternatives will be maintained in the population if variation in female preference ($0 < C < 1$) exists. To predict the existence of male alternatives, we must consider female choice.

Assume that a female's reproductive success differs between the two alternatives only in her immediate reproductive success. Even if female reproductive success (R_I or R_C) might be higher with one male type, the probability of encountering that type of male (f_c or $1 - f_c$) might decrease the expected fitness associated with that preference. Let G denote maximum expected female reproductive success. The fitness values to a female of mating with an intercepting male (W_I) or a courting male (W_C) are:

$$\text{with intercepting males: } W_I = (1 - f_c)R_I \quad (1.4)$$

$$\text{with courting males: } W_C = f_c R_C$$

Thus female fitness is

$$G = \max\{W_I, W_C\} \quad (1.5)$$

In this scenario, only immediate mating success differs between alternatives, and thus neither female nor male behaviour will vary with time. The only parameters in this model are the relative reproductive success of females (R_I and R_C) and the overall mating success of intercepting males relative to courting males, α . Female preference (C) and male frequency (f_C) are variables whose outcome is predicted by the model. Female preference $0 < C < 1$ if $W_C = W_I$, so that

$$f_C = R_I / (R_I + R_C) \quad (1.6)$$

If female fitness is the same whether they mate with intercepting or courting males ($W_I = W_C$), then $C = 0.5$. Since $f_C = C / [(1 - C)\alpha + C]$ and $C = 0.5$, then $f_C = 0.5 / [(1 - 0.5)\alpha + 0.5] = 1 / (1 + \alpha)$. If $C = 0.5$, we must have $1 / (1 + \alpha) = R_I / (R_I + R_C)$ or $\alpha = R_C / R_I$.

Male alternatives will be maintained in the population if females do not have a preference between male alternatives ($C = 0.5$ if $\alpha = R_C / R_I$ and $f_C = 1 / (1 + \alpha)$). When $\alpha = 1$, then $C = f_C = 0.5$ if $R_C = R_I$. If females have higher immediate mating success with courting males, females will prefer courtship and males are predicted to court females ($C = 1$ and $R_I < R_C$ and $f_C = 1$). On the other hand, if female reproductive success is higher with intercepting males, then females will prefer these males and only intercepting males are predicted to occur in the population ($C = 0$, $R_I > R_C$ and $f_C = 0$). If $\alpha < 1$ ($f_C > 0.5$), then the reproductive success of a female mating with an intercepting male must be higher than mating with a courting male (such that $\alpha = R_C / R_I$) for male alternatives to co-exist. In essence, for male alternatives to co-exist, females must achieve higher average reproductive success to compensate for the fact that intercepting males are less common. In contrast, if we did not consider female choice, we would predict that male alternatives would always co-exist at $f_C = 1 / (1 + \alpha)$.

Thus female choice can suppress the existence of male alternatives even when frequency-dependence alone predicts both alternatives in the population. Even small differences in female reproductive success between male types completely alter the predictions. If we did not consider the effect of male behaviour on female fitness, we would not be able to explain the absence of male alternative reproductive behaviours in a species where frequency-dependent fitness alone would predict the stable co-existence of male alternatives. These results are predicted in any situation where male alternatives are negatively frequency-dependent and females choose between male alternatives.

SCENARIO 2: MALE FREQUENCY-DEPENDENT ALTERNATIVES AFFECT FEMALE SURVIVAL AND SUCCESS

We now consider a model where behaviour may depend on time. Consider two species exhibiting the same basic reproductive system with one exception: one of these species breeds continuously, whereas the other breeds during a single reproductive season. In both species, males defend territories where females visit to mate. Other males hover near these sites and mate with any willing females. We refer to these two male behaviours as territory defenders and non-territorial males. Assume that a male's success in obtaining females or a territory is independent of any male characteristic such as size, age or condition. Also assume that a male's fitness is negatively frequency-dependent (Fig. 2) and male survival probability is unaffected by behaviour choice. Let t represent the present time period and T the length (in time periods) of the reproductive period. Let $F(t, T)$ denote the maximum expected male fitness from time t . This is basically the same as in the previous model, except

now present behaviour choice depends also on survival to the next time period and future fitness. The fitness values of a male that is territorial and a male that is non-territorial in the current time period are:

$$\begin{array}{ll}
 \text{non-territorial males: } & V_N(t, T) = (\alpha/(1 - f_D))(1 - C) + \lambda F(t + 1, T) \\
 \text{territory defenders: } & V_D(t, T) = (1/f_D)C + \lambda F(t + 1, T)
 \end{array} \quad (2.1)$$

total fitness present fitness future fitness

Thus male fitness is

$$F(t, T) = \max\{V_N(t, T), V_D(t, T)\} \quad (2.2)$$

Female preference (C) takes the same form as in the previous model. However, imagine that females have greater reproductive success mating with territorial males but that their survival probability is lower, for example because predators attack females at territories ($0 < \lambda_D < \lambda_N < 1$ and $R_N < R_D$). Females, therefore, experience a trade-off between greater reproductive success and lower survival. Assume females encounter many males and are thus unaffected by the frequency of male behaviour types. Let $G(t, T)$ represent the maximum expected female fitness from time t . The fitness values of mating with a non-territorial ($W_N(t, T)$) or a territorial male ($W_D(t, T)$) in t are:

$$\begin{array}{ll}
 \text{with non-territorial males: } & W_N(t, T) = R_N + \lambda_N G(t + 1, T) \\
 \text{with territory defenders: } & W_D(t, T) = R_D + \lambda_D G(t + 1, T)
 \end{array} \quad (2.3)$$

total fitness present fitness future fitness

And female fitness is

$$G(t, T) = \max\{W_N(t, T), W_D(t, T)\} \quad (2.4)$$

A seasonal breeder has a finite amount of time in which reproduction must occur, whereas continuous breeders' reproduction is relatively independent of absolute time, their reproductive season only ending when they die. In terms of the model, the continuous breeder is the case where $T \rightarrow \infty$, and thus there is no probability of an individual surviving from t to T . Even for the seasonal breeder, if T is sufficiently large, there will be a time $t \ll T$ where reproduction will be independent of absolute time. Clearly, in the final time period, females of the seasonal species should always choose to mate with a territorial male because it gives them the highest reproductive success. However, in the case of the continuous breeder, reproduction will be independent of time. When females reproduce repeatedly, they may become relatively risk-averse if the less risky (but lower-success) alternative leads to overall greater fitness (Warner, 1998).

Because we have assumed that only male behaviour type affects female fitness, we can solve the female and male fitness equations analytically (see Appendix 2 for details). We are interested in three questions: First, what differences in survival are required to compensate for a given difference in reproductive success in the case of the continuous breeder? Second, in the seasonally breeding species, might females switch to being risk-averse if the end of their reproductive season is far enough away? We can calculate, for a given difference in reproductive success and survival probability, if females will become risk-averse and, if so, when in the reproductive season this will occur. Third, can we predict the circumstances under which male alternatives are predicted to occur?

First, we calculate the difference in survival probability necessary for females breeding continuously to prefer a low-success less risky alternative (see Appendix 2). When reproduction is independent of time, the following inequality must hold for females to prefer non-territorial males (the less risky but lower immediate-success alternative):

$$\lambda_N R_D - \lambda_D R_N > R_D - R_N \quad (2.5)$$

Even small differences in survival can compensate for reasonably large differences in immediate success (Fig. 3). Thus differences in the length of the reproductive season, through their effect on female choice, can profoundly alter the relative mating success of male alternatives. Despite the fact that male frequency-dependence alone predicts that both behaviours would be maintained in the population, female choice once again alters the basic predictions made by male frequency-dependence. Furthermore, the effect of female choice will depend strongly on the mating system and any other factors that affect the fitness of female choice. Even if we could measure a female's mating success with both male types, we could not explain a female's preference for a lower-success alternative without knowledge of the long-term survival of females mating with both male types.

In the continuous-breeding species, we predict that females will usually prefer the less risky behaviour even for small differences in survival probability (Fig. 3). In contrast, the seasonally reproducing species is predicted to prefer the high-success behaviour near the end of their reproductive season. It is possible to calculate how long during a reproductive season (how many time periods t) it takes for a seasonally reproducing female to prefer the low-risk non-territorial males at the beginning of the breeding season. For a given set

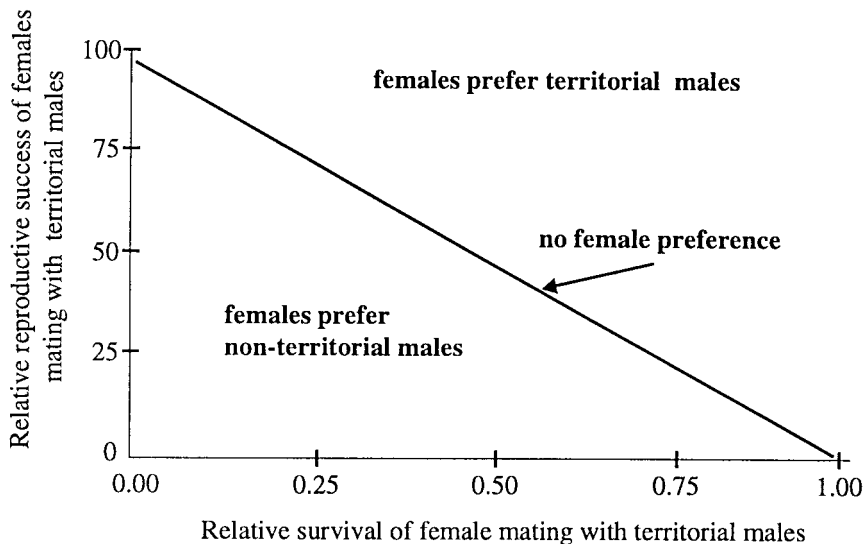


Fig. 3. When reproduction is time-independent (i.e. continuously breeding species), for a given relative reproductive success and survival probability, females will prefer one of two male alternatives. Females will choose non-territorial males below the line and territorial males above the line. For this figure, female reproductive success with non-territorial males $R_N = 1$ and survival probability $\lambda_N = 0.99$.

of reproductive successes (R_N and R_D) and survival probabilities (λ_N and λ_D), the time from the end of the reproductive season (in time periods t_{switch}) before which females will be risk-averse (see Appendix 2; cf. Mangel, 1990b) is

$$t_{\text{switch}} = \ln\left[\frac{(R_N - R_D)(1 - \lambda_D)}{R_N(\lambda_N - \lambda_D)} + 1\right] / \ln(\lambda_D) \quad (2.4)$$

If $t < T - t_{\text{switch}}$, females will be risk-averse. As the relative survival probability of mating with territorial males decreases, the minimum length of the reproductive season in which females will be risk-averse decreases (Fig. 4). For some values, females will always prefer territorial males. Females will prefer non-territorial males if the reproductive success of mating with either alternative is equivalent. Similarly, as the difference in reproductive success increases, the minimum length of the breeding season in which females are risk-averse will increase.

Since male success is affected by female preference, alternatives will only be maintained if female fitness is identical when mating with either alternative and, in the seasonally reproducing species, if females switch from risk-averse to risk-prone during the reproductive season (see Appendix 2). Thus time-dependent variation in female choice can maintain both behaviours in the population. Males may switch between male alternatives with seasonal changes in female preferences. In contrast, in continuously reproducing species, males are predicted to adopt the single behaviour that females prefer. These results will apply to any case where female success and survival are affected by their choice between male alternatives that are negatively frequency-dependent.

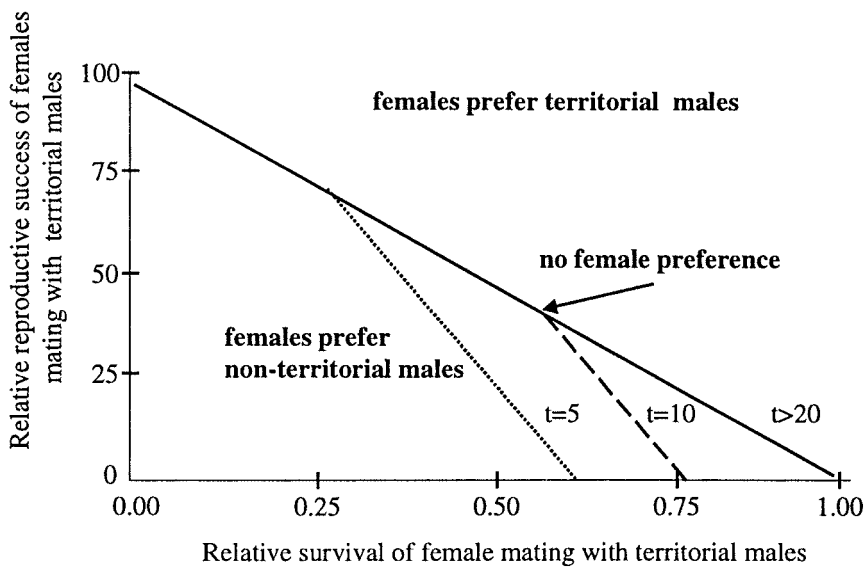


Fig. 4. When reproduction is limited in time (as in some seasonally breeding species), females that would prefer non-territorial males in the time-independent situation (parameter combinations below the solid line) switch to territorial males (i.e. become risk-prone) when there are t remaining time periods in the breeding season. In this figure, each line represents the boundary between parameter values for which, with t remaining time periods in the reproductive season, females will be risk-averse or risk-prone. Here, female reproductive success with non-territorial males is $R_N = 1$ and survival probability $\lambda_N = 0.99$.

SCENARIO 3: MALE ENERGY-DEPENDENT ALTERNATIVES

Condition-dependence is another mechanism that may allow the stable co-existence of male alternatives. There are many ways in which male behaviour might depend on individual size, age, energy reserves, or even experience. Consider a hypothetical species where males call to attract females or are satellites of these calling males. Satellites intercept females who are approaching a calling male. A male's ability to call loudly may be energetically costly (e.g. Arak, 1988). Furthermore, the loudness (and thus the effectiveness) of a male's call may depend on his energetic state (e.g. Arak, 1988; Lucas and Howard, 1995; Lucas *et al.*, 1996). Males with high energy reserves may call loudly and attract many females, while low-energy males are much less successful (Fig. 5). Imagine that satellite males are able to store energy and their immediate mating success is unaffected by their energetic reserves (Fig. 5). In this model, we assume multiple energetic classes exist where satellite males increase in energetic state one level per time period and calling males decrease in energy reserves one level per time period. We let the maximum level of energy be x_{max} and ignore for now the fact that male success might also be frequency- or density-dependent (but see Lucas and Howard, 1995; Lucas *et al.*, 1996). Assuming female preference (C) affects male fitness as in the previous models, let $F(x,t,T)$ denote the maximum expected male fitness in state x from time t . The reproductive values of adopting satellite ($V_S(x,t,T)$) or calling behaviour ($V_C(x,t,T)$) in state x at time t are:

$$\begin{aligned}
 \text{satellite males: } V_S(x,t,T) &= (1 - C) x_{max}/2 + \lambda F(x',t+1,T) & (3.1) \\
 x' &= \min\{x_{max}, x + 1\} \\
 \text{calling males: } V_C(x,t,T) &= C x + \lambda F(x',t+1,T) \\
 x' &= \max\{x_{min}, x - 1\} \\
 & \text{total fitness} \quad \text{present fitness} \quad \text{future fitness}
 \end{aligned}$$

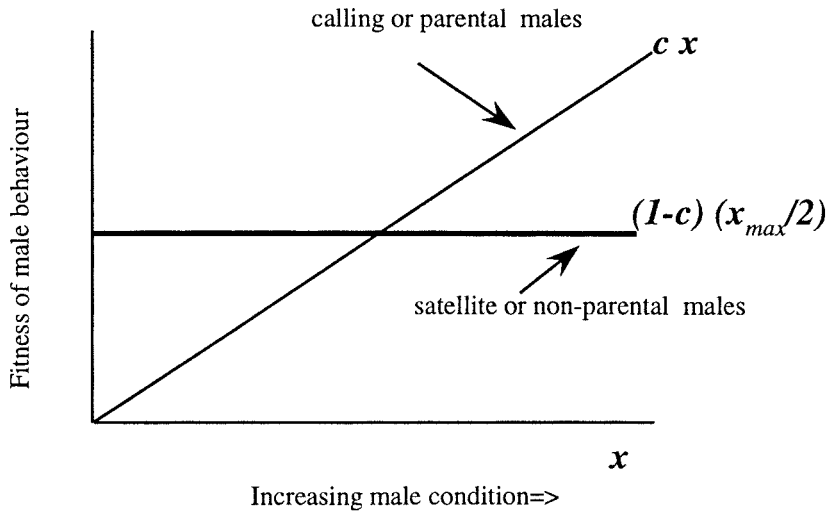


Fig. 5. Condition-dependent fitness of males. One alternative increases linearly with condition while the other is unaffected.

And male fitness is

$$F(x,t,T) = \max\{V_S(x,t,T), V_C(x,t,T)\} \quad (3.2)$$

Male behaviour is energy-dependent, and a male's energy reserves will increase or decrease based on his behaviour.

We assume that female choice does not depend on the frequency of male behaviours in the population. Calling males should be easy to find and satellites are always found nearby. The reproductive success of mating with these male types might differ. Let $G(t,T)$ represent the maximum expected female fitness from time t . The reproductive values of mating with a satellite male ($W_S(t,T)$) or a calling male ($W_C(t,T)$) in time t are:

$$\begin{array}{llll} \text{with satellite males:} & W_S(t,T) = & R_S + & \lambda G(t+1,T) \\ \text{with calling males:} & W_C(t,T) = & R_C + & \lambda G(t+1,T) \\ & \text{total fitness} & \text{present fitness} & \text{future fitness} \end{array} \quad (3.3)$$

And female fitness is

$$G(t,T) = \max\{W_S(t,T), W_C(t,T)\} \quad (3.4)$$

Female fitness (and thus female preference) is only affected by the relative reproductive success they obtain with the two alternative male behaviours. Females are predicted to prefer satellite males ($C=0$) if $R_S > R_C$, calling males ($C=1$) if $R_S < R_C$, and will show no preference ($C=0.5$) if $R_S = R_C$.

For definiteness, imagine that this is a species of frog that breeds continuously. As a result, we can consider male behaviour choices to be unaffected by time in the reproductive season because their breeding season essentially never ends: $T = \infty$. If we were to consider only the energy-dependent fitness without the effect of behaviour choice on energetic state, we would predict that males should switch between satellite behaviour and calling where the condition-dependent fitness curves cross (when $x = x_{\max}/2$; Fig. 5). However, this prediction changes when we solve equation (3.2), which includes males losing energy by calling and gaining energy by being a satellite. Even in the absence of a female preference, males are predicted to be satellites unless their energy reserves are very high. Female choice alters this prediction even further. If females prefer calling males ($C=1$, which occurs where $R_S < R_C$), then males will be satellites if their energy reserves are low and call only if the energy level is at its maximum. However, if females prefer satellite males ($C=0$, which occurs where $R_S > R_C$), all males will adopt the satellite behaviour regardless of energy level.

Male behaviour in this model is driven both by energy reserves and female preference. In this scenario, females can suppress the existence of calling males. However, even when females strongly prefer calling males, males will still adopt the satellite behaviour to increase their energy reserves. Therefore, alternatives can be maintained despite female preference. The effect of female preference on the existence and expression of male alternatives will hold not only for the specific type of species discussed, but in any case where male alternatives are differentially condition-dependent and females choose between male alternatives.

SCENARIO 4: MALE SIZE- AND FREQUENCY-DEPENDENT ALTERNATIVES

Previously, we considered cases where male fitness depended on either the frequency of male behaviours or individual male condition. It is clearly possible, however, that both may occur simultaneously within one population (e.g. Bednekoff and Clark, 1996; Gross, 1996).

Consider as an example a species where some males provide parental care and a male's ability to defend his offspring from predators increases with size. Assume a male's success in defending offspring increases as a linear function of male size. Let x represent a male's size, with the maximum size possible being x_{\max} . Males might also refuse to provide parental care. For these males, offspring survival (and thus reproductive success) should be unaffected by size. In analogy to Fig. 5, the fitness of one alternative is independent of state and the other increases linearly with state. Assume that parental males do not grow when reproductive, but non-parental males increase one size class per time period. Although condition will affect a male's reproductive success, female choice will also influence the probability males will mate. For simplicity, assume that survival is independent of behaviour. However, if most males in the population compete for territories in which to attract females and raise their offspring, the parental males' fitness might be negatively frequency-dependent. Similarly, non-parental males may compete for access to females making their fitness negatively frequency-dependent as well (Fig. 2). Let $F(x, t, T)$ denote the maximum expected fitness of a male of size x from time t . The fitness values of adopting non-parental ($V_{\text{NP}}(x, t, T)$) or parental ($V_{\text{P}}(x, t, T)$) behaviour for a male of size x in time t are:

$$\begin{aligned} \text{non-parental males: } V_{\text{NP}}(x, t, T) &= (\alpha/(1-f_{\text{P}}))(1-C)(x_{\max}/2) + \lambda F(x', t+1, T) \\ x' &= \min\{x_{\max}, x+1\} & (4.1) \\ \text{parental males: } V_{\text{P}}(x, t, T) &= (1/f_{\text{P}})Cx + \lambda F(x, t+1, T) \\ \text{total fitness} \quad \text{present fitness} \quad \text{future fitness} \end{aligned}$$

And male fitness is

$$F(x, t, T) = \max\{V_{\text{NP}}(x, t, T), V_{\text{P}}(x, t, T)\} \quad (4.2)$$

Females must choose between males that provide parental care and those that do not. A female's success in either alternative will depend both on offspring success and the frequency of parental and non-parental males in the population. Female search costs increase as the frequency of the preferred male alternative decreases. If parental males are common and have higher offspring survival, females should prefer parental males. If parental males are rare, however, females may be willing to mate with non-parental males because of search costs. Assume female survival probability is unaffected by their choice of mate. Let $G(t, T)$ represent the maximum expected female fitness from time t . The fitness values of mating with a non-parental ($W_{\text{NP}}(t, T)$) or parental ($W_{\text{P}}(t, T)$) male in time t are:

$$\begin{aligned} \text{with non-parental males: } W_{\text{NP}}(t, T) &= (1-f_{\text{P}})R_{\text{NP}} + \lambda G(t+1, T) & (4.3) \\ \text{with parental males: } W_{\text{P}}(t, T) &= f_{\text{P}}R_{\text{P}} + \lambda G(t+1, T) \\ \text{total fitness} \quad \text{present fitness} \quad \text{future fitness} \end{aligned}$$

And female fitness is

$$G(t, T) = \max\{W_{\text{NP}}(t, T), W_{\text{P}}(t, T)\} \quad (4.4)$$

Females will show no preference ($C = 0.5$) when $W_{\text{NP}}(t, T) = W_{\text{P}}(t, T)$ or $f_{\text{P}} = R_{\text{NP}}/(R_{\text{NP}} + R_{\text{P}})$. Females should prefer non-parental males when f_{P} is smaller and parental males when f_{P} is larger than $R_{\text{NP}}/(R_{\text{NP}} + R_{\text{P}})$.

Solving the male and female fitness equations simultaneously (see Appendix 3 for details) allows us to predict the male behaviour. When females prefer parental males or in the absence of female preference, males are predicted to switch to parental behaviour only when they have grown to a large size. If parental care is facultative and females prefer non-parental males, males will adopt the non-parental behaviour exclusively. If male fitness only depended on female preference and male condition, then males would always be parental when large. However, the inclusion of frequency-dependence allows female preference for non-parental males to suppress the expression of parental behaviour in males completely.

By including female choice in the model, predicted male switch-points and even the occurrence of non-parental males differ from predictions based on only condition- and frequency-dependence. Also, the consideration of either frequency- or condition-dependent fitness alone leads to different predictions than when both mechanisms are considered simultaneously.

SCENARIO 5: FEMALE CONDITION-DEPENDENT CHOICE BETWEEN MALE ALTERNATIVES

We now consider a species where female choice depends on male behaviour and female condition. Imagine a species where some males provide parental care while other males hover around female feeding sites and spawn with willing females. Imagine that females must search for parental males. Searching requires energy which reduces their short-term fecundity. In contrast, non-parental males are always available. However, offspring success is lower with non-parental males. If females vary in fecundity, then female choice might depend on female condition. If the two male alternatives (parental and non-parental) are neither frequency- nor condition-dependent, past theory would predict that both alternatives could not be maintained. In this case male behaviour choice depends only on female preference. Let $F(t, T)$ = maximum expected male reproductive success. If the fitness value of either male behaviour is given by

$$\begin{array}{llll} \text{non-parental males:} & V_{\text{NP}}(t, T) = & (1 - C) + & \lambda F(t + 1, T) & (5.1) \\ \text{parental males:} & V_{\text{P}}(t, T) = & C & + & \lambda F(t + 1, T) \\ & & \text{total fitness} & \text{present fitness} & \text{future fitness} \end{array}$$

then male fitness is

$$F(t, T) = \max\{V_{\text{NP}}(t, T), V_{\text{P}}(t, T)\} \quad (5.2)$$

Imagine that if females search for a parental male there is an associated search cost S . Further assume that the reproductive success of mating with a non-parental male is always lower than mating with a parental male ($R_{\text{NP}} < R_{\text{P}}$). Female choice will be affected by their own fecundity (x), the intrinsic reproductive success of mating with a parental or non-parental male (R_{NP} and R_{P}), and the cost of searching for parental males (S). Assume that female fecundity, determined by feeding success, is relatively random and completely unaffected by their choice between male types. Let $G(x, t, T)$ represent the maximum expected female fitness for a female of fecundity x in time t . The fitness values of mating with a non-parental ($W_{\text{NP}}(x, t, T)$) or parental male ($W_{\text{P}}(x, t, T)$) in state x at time t are:

$$\begin{array}{ll}
 \text{with non-parental males: } & W_{\text{NP}}(x,t,T) = (R_{\text{NP}}x) + \lambda G(x,t+1,T) \quad (5.3) \\
 \text{with parental males: } & W_{\text{P}}(x,t,T) = (R_{\text{P}}x) - S + \lambda G(x,t+1,T) \\
 & \text{total fitness} \quad \text{present fitness} \quad \text{future fitness}
 \end{array}$$

And female fitness is

$$G(x,t,T) = \max\{W_{\text{NP}}(x,t,T), W_{\text{P}}(x,t,T)\} \quad (5.4)$$

As a result of the female fecundity-dependent fitness, females will vary in their preference. Females will prefer parental males when $x > x_{\text{switch}}$, where

$$R_{\text{NP}}x_{\text{switch}} = R_{\text{P}}x_{\text{switch}} - S \quad (5.5)$$

or

$$S/(R_{\text{P}} - R_{\text{NP}}) = x_{\text{switch}} \quad (5.6)$$

The fecundity at which females search for parental males will increase as the cost of searching or the benefit of mating with a parental male increases (Warner *et al.*, 1991; Luttberg and Warner, in press). The resulting variation in female mate choice can maintain male alternatives even in the absence of condition- or frequency-dependent fitness due to interactions between males. As the intrinsic reproductive success of mating with a parental male increases, females of lower fecundity will be willing to search for parental males. As female preference changes, so will the frequency of male alternatives in the population. The exact frequency of parental and non-parental males in the population will be determined by the variation in female choice and female fecundity. This model indicates that any factors causing variation in female choice (such as age, condition, quality, experience or energy limitations) have the potential to allow the stable co-existence of male alternatives even in the absence of traditional male frequency- or condition-dependence.

GENERAL CONCLUSIONS

Female choice can completely alter the predictions made by simply considering frequency- or condition-dependence within males (Table 1). Female choice may suppress the existence of male alternatives completely or alter their exact pattern of expression. Furthermore, variation in female choice caused by female condition-dependence can maintain male alternatives at equilibrium when neither frequency- nor condition-dependent male reproductive success exists. Although we have focused our discussion on a few hypothetical examples, the models can be interpreted much more broadly. They clearly demonstrate the importance of female choice and conflict between the sexes in the pattern or existence of male alternatives.

To explain the co-existence of male alternatives, we usually study male behaviour and look for frequency- or condition-dependence. Imagine that none of the factors which usually explain the co-existence of alternatives seem to occur. We might conclude that the variation is neutral or argue that genetic constraints exist. The stable co-existence of male alternatives can also simply be explained by variation in female choice. If females vary in their mate choice, male alternatives can be maintained without any other explanation necessary. In contrast, we might also wish to explain the absence of male alternatives in a species where male fitness is frequency- and condition-dependent. The models clearly

Table 1. Summary of the model predictions

Scenario	Ignoring female choice	Considering female choice
1. Static frequency-dependence	Alternatives co-occur and are stable at the frequency where the negative frequency-dependent male fitness curves cross	Male alternatives only occur if females show no preference between male alternatives
2. Dynamic frequency-dependence (females trade-off survival and mating success)	Same as above	Male alternatives occur when female preference is time-dependent, or if females show no preference between male alternatives
3. Dynamic energy-dependence	Alternatives co-occur and males switch between behaviours when energy reserves are high	Female preference can suppress the occurrence of the energetically costly alternative, but not the low-energy alternative
4. Dynamic frequency-dependence and size-dependence	Alternatives co-occur and males switch between behaviours when large	Female preference can suppress the occurrence of the large-size alternative, but not the small-size alternative
5. Female condition-dependence	Male alternatives not predicted	Female variation in choice acts as a mechanism for maintaining male alternatives

indicate that it is possible for female preference to suppress the stable co-existence of male alternatives, even if male frequency- and condition-dependence would allow them to co-exist.

In a Mediterranean wrasse, *Symphodus tinca*, females choose between parental and non-parental males (Warner *et al.*, 1991). In this species, parental care is facultative (van den Berghe, 1990, 1992) and female choice depends on the frequency of parental males in the population, on search costs and on the relative fitness obtainable from the two types (Warner *et al.*, 1991). This species could represent an example of variation in female choice allowing the stable co-existence of two alternatives. In another closely related species, *S. ocellatus*, females prefer not to mate with sneaking males but are unable to avoid them altogether (Lejeune, 1985; Taborsky *et al.*, 1987; van den Berghe *et al.*, 1989). In this species, females are not able to exert complete control over mate choice because spawning is external.

The mating system and reproductive biology may limit the degree to which females control mate choice and thus influence the evolution of alternatives. Clearly, the potential exists for females to choose between male alternatives and thus influence their evolution and pattern of expression. Future empirical studies should examine the influence of changes in female choice on the fitness of male alternatives and the frequency with which males adopt alternatives. Also, studies should also examine variation in female choice as a mechanism allowing the stable co-existence of male alternatives. Future models must focus on more realistic forms of female choice in an attempt to determine factors that increase or decrease the influence a female exerts on the evolution and expression of male alternatives.

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APPENDIX 1: METHOD FOR SOLVING A MULTI-PLAYER DYNAMIC STATE VARIABLE GAME

Dynamic state variable games are solved using a best response method (Mangel, 1990a; Mangel *et al.*, 1994; McNamara *et al.*, 1997; Clark and Mangel, 1999). This means that the algorithm finds the best response to the strategy adopted by the population. For example, if the entire population of males is displaying at one site, a mutant that displayed from a different site might experience less competition and therefore higher mating success. Imagine there are two sites that attract equal numbers of females. The best response to the population strategy ‘display from site 1’ might be to display from site 2. We then find the best mutant response if the entire population displays from site 2. To find the stable strategy (or ESS), this iterative process is repeated until the best response to the population strategy is to adopt the population strategy. For example, the best response to ‘display with equal probability from both sites’ would be to do the same, since competition and mating success would be equal at both sites. Let π represent a population strategy and $B(\pi)$ represent the best response to the strategy π . Then, in a given iteration n :

$$B(\pi_n) = \pi_{n+1} \quad (\text{A1.1})$$

To find the equilibrium, one repeats this process until

$$B(\pi^*) = \pi^* \quad (\text{A1.2})$$

We extend this process to examine a game between males and females. Consider the above example, but now assume that females also choose between sites. If most of the females are at site 1 and most of the males are at site 2, the best female mutant response to that population strategy might be to go to site 1 where there are more males to choose from and less competition with other females. Let π be the male strategy and γ be the female strategy. The best female response strategy if the population of males adopts π and the population of females adopts γ will be

$$B_{f}(\pi_n, \gamma_n) = \gamma_{n+1} \quad (\text{A1.3})$$

And for males the best response is

$$B_m(\pi_n, \gamma_n) = \pi_{n+1} \quad (\text{A1.4})$$

The equilibrium occurs where

$$B_m(\pi^*, \gamma^*) = \pi^* \quad \text{and} \quad B_f(\pi^*, \gamma^*) = \gamma^* \quad (\text{A1.5})$$

In other words, both stable male and female strategies are found where the best response to both the male and female population strategies is to adopt the population strategy for that sex. For example, the stable female strategy might be to split your time equally between site 1 and 2 and the best male response is to be evenly distributed between site 1 and 2. Then a female or male mutant would not have higher mating success if they adopted a different strategy.

We use a computer algorithm to solve the linked fitness equations and find the stable strategy for males and females. First, we make an initial guess for both male and female population strategies π_0 and γ_0 and generate as a result of those strategies the environment any mutant would experience (e.g. the frequency of males and females at both sites). We then find the best response to these initial strategies $B_f(\pi_0, \gamma_0) = \gamma_1$ and $B_m(\pi_0, \gamma_0) = \pi_1$ and calculate the environmental parameters that result from γ_1 and π_1 . These two steps are repeated until we find $\pi_n \cong \pi_{n-1}$ and $\gamma_n \cong \gamma_{n-1}$. It is also possible that the algorithm will not converge to find stable strategies.

Although we have focused on a game between males and females, the same algorithm applies for any two-player game. This method could also clearly be extended for multiple players. However, it may be difficult to find a stable set of strategies for games with many different players. Ways to stabilize dynamic state variable games are described by McNamara *et al.* (1997) and Clark and Mangel (1999). If stochastic processes are considered in the forward iteration, then one must use stability criteria that do not require the behaviour matrix to be identical between iterations of the model. In the models discussed here, forward iterations were not stochastic. One must also bear in mind that this type of game has only been solved analytically for a single case of a one-player game (McNamara *et al.*, 1997).

APPENDIX 2: ANALYTICAL SOLUTION OF SCENARIO 2

If female fitness is not affected by female condition or the frequency of male behaviours in the population, then the female fitness equation can be solved analytically (Mangel, 1990b). The reproductive success of repeating one behaviour for t time periods with the immediate reproductive success R and the survival to the next time period λ for t time periods is

$$\begin{aligned} F(1, t) &= R + \lambda F(2, t) \\ &= R + \lambda(R + \lambda F(3, t)) \\ &= R(1 + \lambda^2 + \lambda^3 + \lambda^4 + \dots + \lambda^{t-1}) \\ &= R(1 - \lambda^t)/(1 - \lambda) \end{aligned} \quad (\text{A2.1})$$

As $t \rightarrow \infty$,

$$F(1, t) \rightarrow R/(1 - \lambda) \quad (\text{A2.2})$$

We have two behaviours with the associated immediate reproductive success $R_N < R_D$ and the survival probabilities $\lambda_N > \lambda_D$. At the final time period, since there is no future fitness, females should prefer the high-success, high-risk mating option. For earlier time periods, higher overall fitness may be associated with a preference for the safer behaviour, even though it has lower immediate mating success. First, consider the situation where t is infinite (or where behaviour becomes independent of time). Females mating with non-territorial males will have higher total fitness if

$$R_N/(1 - \lambda_N) > R_D/(1 - \lambda_D) \quad (\text{A2.3})$$

which simplifies to

$$\lambda_N R_D - R_N \lambda_D > R_D - R_N \quad (\text{A2.4})$$

We can now predict the survival probability of mating with a non-territorial male required to outweigh a given difference in reproductive success (Fig. 3). The two behaviours will have equal fitness when

$$R_D = R_N [(1 - \lambda_D)/(1 - \lambda_N)] \quad (\text{A2.5})$$

In this case, females will have no preference between male alternatives and $C = 0.5$. Since the frequency of the male alternatives is $f_C = C/[(1 - C)\alpha + C]$ and $C = 0.5$, $f_C = (1/1 + \alpha)$ and both male alternatives will occur in the population. If females prefer non-territorial males in the time-independent case, and yet females have a higher immediate reproductive success when mating with territorial males, there must be some point in the reproductive season where females go from risk-averse to risk-prone. The fitness of mating repeatedly with a territorial male for t time periods is given by the equation

$$R_D [(1 - \lambda_D)^t / (1 - \lambda_D)] \quad (\text{A2.6})$$

If females switch from mating with non-territorial males with t_{switch} time periods remaining in the reproductive season, their fitness will be

$$R_N + \lambda_N R_D [(1 - \lambda_D^{t_{\text{switch}}}) / (1 - \lambda_D)] \quad (\text{A2.7})$$

For females to switch to mating with non-territorial males, their mating success must be higher mating in time t_{switch} with non-territorial males. This will be true if

$$R_N + \lambda_N R_D [(1 - \lambda_D^{t_{\text{switch}}}) / (1 - \lambda_D)] > R_D + \lambda_D R_D [(1 - \lambda_D^{t_{\text{switch}}}) / (1 - \lambda_D)] \quad (\text{A2.8})$$

To find the period at which females become risk-averse, we solve equation (A2.8) for t_{switch} :

$$t_{\text{switch}} = \ln[((R_N - R_D)(1 - \lambda_D)) / (R_D(\lambda_N - \lambda_D) + 1)] / \ln(\lambda_D) \quad (\text{A2.9})$$

The value of t_{switch} will always be positive for the conditions $0 < \lambda_D < \lambda_N < 1$ and $R_N < R_D$. For t_{switch} to be positive, we must have

$$0 > ((R_N - R_D)(1 - \lambda_D)) / (R_D(\lambda_N - \lambda_D)) \quad (\text{A2.10})$$

This will always be true because $0 < R_N < R_D$ and $0 < \lambda_N < \lambda_D < 1$. Therefore, for any reproductive season longer than t_{switch} , females will switch from preferring non-territorial males to territorial males when there are t_{switch} time periods remaining in the breeding season. Since male alternatives can be maintained where $f_C = C/[(1 - C)\alpha + C]$ and $0 < C < 1$, male alternatives will be maintained when female fitness is equal with both male alternatives and $C = 0.5$. Male alternatives will also be maintained when C switches at t_{switch} from $C = 0$ to $C = 1$ because the average female preference over the reproductive season will be $0 < C < 1$, allowing the maintenance of alternatives within the population.

APPENDIX 3: NUMERICAL SOLUTIONS

Using analytical solutions to test numerical methods. Whenever possible, we solved the models analytically. In Scenarios 1 and 2, analytical solutions are possible. For these scenarios, we also ran the dynamic state variable computer algorithms. Numerical predictions matched the analytical predictions completely. The other dynamic games could only be solved numerically.

The game method. The dynamic programming game is solved using the same basic method as in Houston and McNamara (1987). Using the behaviour matrices resulting from the backward iteration,

a forward simulation calculates the proportion of females preferring one male alternative C and the proportion of males choosing one male alternative f . In the case of state-dependent behaviour, we calculated the average preferences or male frequencies given the state frequency and the behaviour chosen in that state. We then used these parameters (C and f) in another backward iteration of the male and female equations. This iteration procedure was continued until all behavioural matrices and the variables C and f did not change between successive iterations; this behaviour is stable against invasion. Our algorithm was written to conduct a maximum of 1000 runs of the model before declaring the model unstable. Although dynamic games can fail to converge, this was not a problem in any of the cases we considered.

Initiating the game. To start the iteration procedure, we assumed that both females and males showed no preference between the alternatives ($C = 0.5$ and $f = 0.5$). Our final results did not differ if other assumptions were made. We assumed males (Scenarios 3 and 4) or females (Scenario 5) were uniformly distributed between states at $t = 1$. The results presented are only for those time periods after which the state distribution had stabilized and was independent of t . The state distribution for $t > 1$ is determined by individual behaviour choices and the state changes as a result of that behaviour. Only in Scenario 5, where female state did not change, were the final results affected by the assumption made about the initial state distribution. All distributions were calculated based on proportion of individuals in the state rather than simulating the actual number of individuals.

State variables. We assumed $x_{\min} = 1$ and $x_{\max} = 10$. However, we also examined situations where the maximum was smaller ($x_{\max} = 5$) and larger ($x_{\max} = 20$). The qualitative results were unaffected.

Time variables. We made no explicit assumptions about the length of a time period. It must represent sufficient time for a female to choose and mate with a male. A realistic length for t will depend on the species being considered. We always allowed T to be large enough that the behaviour at $t \ll T$ was independent of time. In all cases, $T = 1000$ was sufficient to find stationarity. The results we present are for time periods $t \ll T$ only unless otherwise stated. For each scenario, we assumed that male and female fitness in the final time period $F(x, T, T) = 0$ and $G(x, T, T) = 0$.

Frequency-dependent functions. Frequency-dependent functions were a part of the male fitness equation in Scenarios 1, 2 and 4. For male frequency-dependence, we assumed the basic form of the function (Fig. 2). We examined a range between 0 and 1 in 0.1 intervals for α . We also considered a linear function of f . Results did not differ significantly.

Condition-dependent functions. Condition-dependent functions were used in Scenarios 3 and 4 in the male fitness equation and in Scenario 5 in the female fitness equation. These functions always took the form described in Fig. 5. Other possibilities were also considered, but the qualitative results were not affected as long as one alternative increased as a function of state while the other was either independent or decreased as a function of state.

Reproductive success variables. For all of the scenarios, female reproductive success differed between male alternatives (Scenario 1: R_I and R_C ; Scenario 2: R_D and R_N ; Scenario 3: R_S and R_C ; Scenarios 4 and 5: R_{NP} and R_P). Only relative differences affected behaviour. As a result, we fixed one value (e.g. R_I) and varied the other (e.g. R_C) from 0 to 1 in intervals of 0.1 and from 1 to 100 in intervals of 1. Predictions were only affected by the direction of the difference unless mentioned specifically. The predictions were not affected by switching the parameter that was fixed.

Survival probability. Unless mentioned explicitly, for the results presented here, we assumed that the survival probability was equal for all behaviour choices and was set at $\lambda = 0.99$. We also ran the models with $\lambda = 0.95$ and the results remained the same.

Stabilizing the model. We used a method proposed by McNamara *et al.* (1997) to stabilize dynamic state variable game models. This was especially necessary for the models examining multiple conflict interactions simultaneously. The method has two parts. First the change in behaviour is damped between iterations. This is achieved by allowing only some portion (δ) of the population to change behaviour between successive runs of the model. The damping increased as the number of iterations searching for a stable behaviour increased ($\delta = 1/\text{number of runs}$). So, for any given iteration, the behaviour adopted by the population $\pi_n = \delta B(\pi_{n-1}) + (1 - \delta)\pi_{n-1}$. The second part of the method allows the behaviour predicted to be a probability of adopting a specific behaviour (e.g. calling). This method assumes that animals make errors when adopting behaviours, and that the probability of making an error is a function of the difference in fitness values. Let $G_\epsilon(x)$ be the probability of adopting a specific behaviour (e.g. calling), where Δv is the difference in expected fitness values (e.g. between calling and being a satellite $\Delta v = V_C(x, t, T) - V_S(x, t, T)$) and ϵ determines the degree of error-making. $G_\epsilon(\Delta v) = 0.5$ when $\Delta v = 0$. If calling and being a satellite have equal fitness values, the predicted probability of calling would be 0.5. We use the function $G_\epsilon(\Delta v) = e^{\epsilon \Delta v} / (e^{-\epsilon \Delta v} + e^{\epsilon \Delta v})$ and $\epsilon = 5$. This method and the exact value of the error and damping parameters only affected the ability of the algorithm to find a solution, not the solution itself.

Determining the effect of female choice on male alternatives. To examine the effect of female choice on male alternatives, we also solved the male equations with a fixed female preference of $C = 0.5$. These predictions were then compared to the predictions made when female choice was allowed to vary in the model.