Evolution of alternative mating tactics: conditional versus mixed strategies

Stewart J. Plaistow,[a] Rufus A. Johnstone,[b] Nick Colegrave,[c] and Matthew Spencer[d]
[a]Laboratoire Ecologie-Evolution (UMR CNRS 5561), Université de Bourgogne, France, [b]Department of Zoology, University of Cambridge, UK, [c]Institute of Cell, Animal, and Population Biology, University of Edinburgh, UK, and [d]Department of Biochemistry, University of Cambridge, UK

Intrasexual polymorphisms have evolved in a wide range of organisms. Most of them have been interpreted as the product of conditional strategies in which the tactic an individual adopts is determined by some aspect of state (e.g., age, size, condition). However, there are a few examples that appear to represent an evolutionarily stable mixture of heritable pure strategies that are maintained by frequency-dependent selection. In the present study, we produce a model of a mating system with two morphs: a territorial morph and a sneak morph. By varying the costs and limits associated with conditional strategies, mating skew, and the proportion of matings obtained by sneaking males, we examine the conditions that favor the evolution of conditional versus pure strategies. Contrary to current thinking, our results show that as long as either costs or limits are greater than zero, conditional strategists are never able to entirely replace pure strategists, and equilibrium populations may frequently consist of a mixture of conditional and pure strategists. Our results suggest that conditional strategists will be most frequent at intermediate levels of mating skew. Polymorphisms in which conditional strategists are rare or absent are most likely to evolve when mating skew is extremely high, the costs and limits of plasticity are very high, or the benefits of being conditional are very low. The limited data available suggest that high mating skew is probably the most important factor. *Key words:* alternative strategies, conditional strategies, costs of plasticity, mating competition, mating skew, polymorphism, tactics. *[Behav Ecol 15:534–542 (2004)]*

Males often use more than one tactic to gain access to females (Austad, 1984; Caro and Bateson, 1986; Gross, 1996; Shuster, 1989; Widemo, 1998). Commonly, some males adopt a territorial tactic and attempt to monopolize access to females whilst other males use a more surreptitious or "sneaky" tactic in which they try to mate with females without defending a resource (see Gross, 1996). Evolutionary game theory initially provided two major explanations for the maintenance of alternative mating tactics: a mixed evolutionary stable strategy (ESS; Maynard Smith, 1982), with alternative tactics maintained by frequency-dependent selection, and a conditional strategy in which the tactic an individual adopts depends upon some aspect of its (environmental or physiological) state (Dawkins, 1980; Gross, 1996). Considerable empirical work has been expended on trying to determine which of these mechanisms explains the existence of alternative mating tactics in particular natural systems (for review, see Andersson, 1994; Gross, 1996). Intuitively, a conditional strategy in which an individual can choose the tactic which best suits its state should be favored. Indeed, most game theory models support the idea that if individuals differ in state, and the pay-off to each tactic depends on state, individuals should always evolve conditional strategies (Hammerstein, 1981; Parker, 1974; Selten, 1980). Most empirical results have been interpreted as supporting this intuition (see Gross, 1996). Examples include male dimorphisms in some scarab dung beetles (Eberhard, 1982; Emlen, 1994), alternative mating tactics in calopterygid damselflies (Forsyth and Montgomerie, 1987; Plaistow, 1997; Plaistow et al., 1996), inducible defence structures in invertebrates (Harvell, 1986;

Lively, 1986b), dispersal polymorphisms (Zera and Denno, 1997), social castes in the hymenoptera (Holldobler and Wilson, 1990; Wheeler and Nijhout, 1983; Wilson, 1971), and seasonal polymorphisms in butterflies (Hazel and West, 1982; Shapiro, 1976).

However, there are at least a few suggested examples of mixed ESSs in which pure strategies are genetically determined. These include birds (Lank et al., 1995), lizards (Sinervo and Lively, 1996), isopods (Shuster et al., 1991), fish (Ryan et al., 1992), rewardless orchids (Gigord et al., 2001), and insects (Tsubaki et al., 1997; Plaistow, Tsubaki, Hooper, and Siva-Jothy, in preparation), although only a few of these studies have demonstrated that the alternative strategies are maintained by frequency-dependent selection (Gigord et al., 2001; Sinervo and Lively, 1996).

In this article, we produce a model aimed at understanding the circumstances that favor the evolution of conditional and pure strategies. It has previously been suggested that deleterious consequences of plasticity may constrain the evolution of conditional strategies (DeWitt et al., 1998; Lively, 1986a; Moran, 1992; Van Tienderen, 1991; Wilson and Yoshimura, 1994). Following the method of DeWitt et al. (1998), we distinguish between costs and limits. Costs such as energy expended on the machinery enabling plastic development directly reduce fitness whatever tactic is adopted. In contrast, a limit reduces a plastic individual's ability to successfully use one of the tactics. For example, a reduction in the quality of an individual might reduce its competitive ability, and thus its success as a territorial individual, but might have no effect on its success as a sneak because the payoff to sneaks does not depend on their ability to compete.

We also include the effect of mating skew, determined by the intensity of competition for territories and the total proportion of matings obtained by individuals adopting the sneak tactic. We show that conditional strategies are most likely at intermediate levels of mating skew, with low costs and

Table 1
Symbols used in the model

Symbol	Explanation
c	Ratio of males to territories
f_C	Proportion of conditional males in population
f_S	Proportion of fixed sneak males in population
f_T	Proportion of fixed territorial males in population
k	Fitness cost of conditionality (proportional reduction in payoff incurred by conditional players, regardless of which tactic they adopt)
p	Threshold quality rank above which a conditional male becomes territorial (and therefore proportion of conditional males that are territorial)
Q	Competitive ability of a male
q	Standardized quality rank (quality) of a male
s	Total fraction of matings claimed by sneaks
$S(q)$	Proportion of males that compete and are stronger than an individual of quality q
U	Average uncertainty of an observer regarding the tactic a randomly chosen individual will adopt
v	Expected payoff to a male that succeeds in acquiring a territory
w_C	Expected payoff to a conditional male
w_S	Expected payoff to a fixed sneak male
w_T	Expected payoff to a fixed territorial male
x	Proportional reduction in quality rank (limit) incurred by conditional males

limits. Conversely, extremes of mating skew and high costs or limits favor pure strategies. Under a wide range of circumstances, conditional and pure strategies can coexist in the same population.

THE MODEL

Consider a population in which males may adopt one of two alternative mating tactics: they may either compete for control of a mating territory or refrain from competition and attempt to obtain matings by subterfuge. We will refer to these possibilities as territorial and sneak tactics. We assume that individuals make a single irreversible decision as to their lifetime tactic at some point during their development (i.e., they cannot change from one tactic to another).

Not all territorial individuals will succeed in obtaining a territory. We assume that individual males vary in their competitive ability, denoted Q, which is distributed according to the probability density function $f(Q)$ $[= F'(Q)]$. For simplicity, we will describe individuals in terms of their standardized quality rank $q = F(Q)$. Thus, a value of $q = 0.5$ implies that a male is competitively inferior to 50% of the population, whereas a value of $q = 0.75$ implies that a male is competitively inferior to only 25% of the population (note that all symbols are defined in Table 1). Focusing on quality rank means that we do not need to specify the precise form of the distribution $f(Q)$, because q will be evenly distributed between zero and one regardless. Thus, our results will apply generally to any to distribution where all males differ in quality.

The ratio of males in the population to available territories will be denoted c (the higher the value of c, the more intense the mating competition). Each territorial male attempts to claim a single, randomly selected territory; if several males contest the same territory, we assume that the individual with the greatest competitive ability succeeds in claiming it.

Overall, we assume that sneaks claim a total fraction s of the matings in the population (regardless of their frequency); the average number of matings obtained by an individual sneak is thus inversely proportional to the fraction of males that adopt the sneak tactic. Successful territorial males claim the remaining fraction $1 - s$ of the matings in the population; again, the average number of matings obtained by an individual successful territorial is thus inversely proportional to the fraction of males that obtain a territory. Unsuccessful territorial males obtain no matings.

A life-history strategy, in our terminology, specifies what tactic a male will adopt (sneak or territorial). "Fixed" strategies specify a single choice of tactic—all males that follow a fixed sneak strategy adopt sneak tactics, and all males that follow a fixed territorial strategy adopt territorial tactics. However, we will also allow for conditional strategies, which specify alternative tactics according to a male's competitive ability. A male that follows a conditional strategy adopts the territorial tactic if its competitive ability q exceeds some threshold value p, and otherwise adopts the sneak tactic (note that because q is evenly distributed between zero and one, p represents the proportion of individuals playing the conditional strategy in question that adopt sneak tactics). There are thus many possible conditional strategies, differing in the threshold value p that they specify. It is not necessary for a conditional male to assess its own competitive rank relative to others when deciding which tactic to adopt. Rather, we assume that there is some physiological switch point that can be optimized by selection, that there is some physiological variable when young that's a good predictor of competitive ability when mature, and that the distribution of competitive ability is stationary (over generations).

We assume that developmental flexibility may entail fitness costs; thus, the payoff to a conditional strategist will be devalued by a proportion k (regardless of the tactic it finally adopts). Moreover, plasticity may limit development; thus the competitive ability of a conditional strategist will be devalued by a proportion x when determining who wins a contested territory.

Calculating payoffs

Given our assumptions, what are the expected payoffs obtained by males that follow different strategies? Consider a population comprising proportions f_S, f_T, and f_C of fixed sneak strategists, fixed territorial strategists, and conditional strategists, in which a proportion p of the last type become sneaks. The expected payoff to an individual sneak in such a population, denoted w_S, is given by

$$w_S = \frac{s}{f_S + pf_C},\qquad(1)$$

i.e., the total fraction of matings claimed by sneaks s, divided by the fraction of males that adopt such tactics (which includes fixed sneaks and conditional males of low competitive ability).

The expected payoff to a territorial male requires a little more effort to calculate. However, as we show in the Appendix, it is given by

$$w_T = v \int_{q=0}^{q=1} \mathrm{Exp}[-cS(q)]\mathrm{d}q,\qquad(2)$$

where v, which denotes the expected payoff to a male that successfully acquires a territory, and $S(q)$, which denotes the proportion of males that compete and are stronger than an individual of quality q, are defined in the Appendix. The payoff to a conditional male is given by

$$w_C = (1 - k)\left(p\frac{s}{fs + pf_C} + v\int_{q=p}^{q=1} \text{Exp}[-cS((1 - x)q)]\mathrm{d}q\right).$$

(3)

Searching for solutions

Having calculated the payoffs to the three types of player, we can attempt to determine the equilibrium solution of the model.

Equilibria featuring only fixed strategies

We begin by considering the conditions under which a mixed equilibrium exists that features only fixed strategies, that is, sneaks and territorials. As derived in the Appendix, the stable frequencies of the two types at such an equilibrium are given by $f_S = s, f_T = 1 - s$, and this mixture of sneaks and territorials is immune to invasion by conditional mutants unless costs and limits are sufficiently small (the precise levels of cost and limit below which conditional mutants can invade, which depend on the other model parameters, are derived in the Appendix and illustrated in the Results).

Equilibria featuring only conditional strategies

What about the possibility of an equilibrium at which all individuals adopt a conditional strategy (i.e., $f_C = 1, f_S = f_T = 0$)? We show in the Appendix that an arbitrarily small cost or limit associated with conditionality is sufficient to render such a purely conditional equilibrium unstable. Only when $x = k = 0$, implying no cost or limit, is a conditional equilibrium possible.

Equilibria featuring both conditional and fixed strategies

Where neither a purely fixed nor a purely conditional equilibrium exists, we must consider the possibility of a mixed equilibrium featuring both conditional individuals and fixed players, either sneaks or territorials (or both). Unfortunately, we are unable to derive explicit analytical solutions for the conditions under which such equilibria are stable, or for the frequencies of the different strategies at such equilibria. Numerical results (based on procedures outlined in the Appendix) are therefore presented in the next section.

RESULTS

Which strategies can coexist?

The parameter space of cost (k) and limit (x) can be divided into regions corresponding to different types of equilibrium solution (Figure 1). Where both costs and limits are high (the upper right-hand part of the space), the conditional strategy is unable to invade, and the fixed sneak and territorial strategies coexist at equilibrium. In a narrow band of intermediate costs and limits, all three strategies coexist. In the lower lefthand part of the space, where both costs and limits are low, the sneak strategy is eliminated and the conditional and territorial strategies coexist. However, there is no region in which the equilibrium consists purely of a conditional strategy, provided that either the cost or the limit is greater than zero.

Effects of mating skew on invasion of the conditional strategy

When c (the number of males per available territory) is large, there are many males per territory, but only one male per territory can succeed. Mating success is therefore very
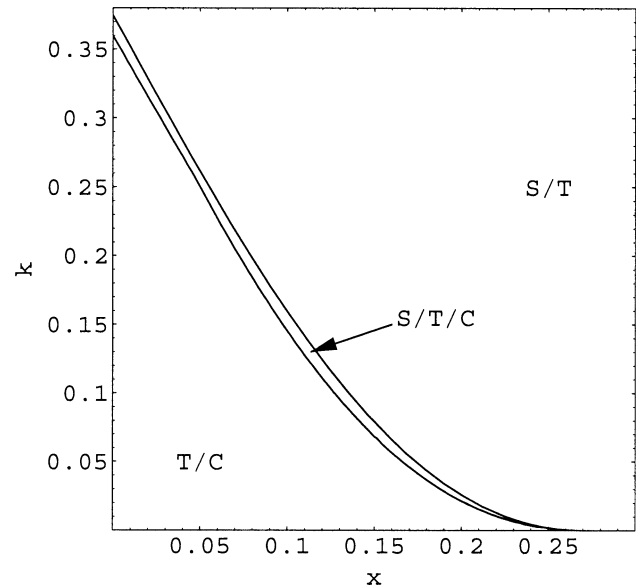

Figure 1
The effect of parameters x (the reduction in competitive ability suffered by conditional strategists) and k (the fixed cost suffered by conditional strategists) on the nature of the equilibrium. When both x and k are sufficiently high (upper righthand corner of the graph) the equilibrium features a mixture of sneaks and territorials; when both x and k are sufficiently low (lower lefthand corner of the graph) the equilibrium features a mixture of territorials and conditional strategists; in a narrow band of parameter values between these two regions, the equilibrium features all three types: sneaks, territorials and conditional strategists. Other parameter values used to generate this figure were $s = 0.25$ and $c = 10$ (note that the boundary of the S/T region of the graph is given by Equation A12 in the Appendix; the boundary between the S/T/C and T/C regions was estimated by numerically calculating model solutions for many different combinations of x and k).

unevenly distributed (over all males), there is intense competition for territories, and competitive ability is a very important determinant of fitness. The range of conditions under which the conditional strategy can invade a population of sneaks and territorials is affected by changing c (Figure 2a). As c increases (successively darker lines on Figure 2a), the limit x on condition of conditional males becomes more important, because competition for territories becomes more intense and the level of competitive ability required to hold a territory increases. However, the cost k paid by all conditional individuals becomes less important as c increases, because the large payoff obtained by those conditional individuals holding territories compensates for the cost.

Similarly, when s (the proportion of total matings obtained by sneaks) is small, most of the fitness obtained by the conditional strategy will come from territorial rather than sneak tactics. Thus small s increases the importance of success in competition, limits become more important and costs less important as determinants of the ability of the conditional strategy to invade (successively darker lines on Figure 2b). Because increasing c and decreasing s both increase the unevenness of the distribution of mating success over all males, they both increase the importance to the conditional strategy of success in competition. However, the ability of the conditional strategy to invade is affected more strongly by c than by s.
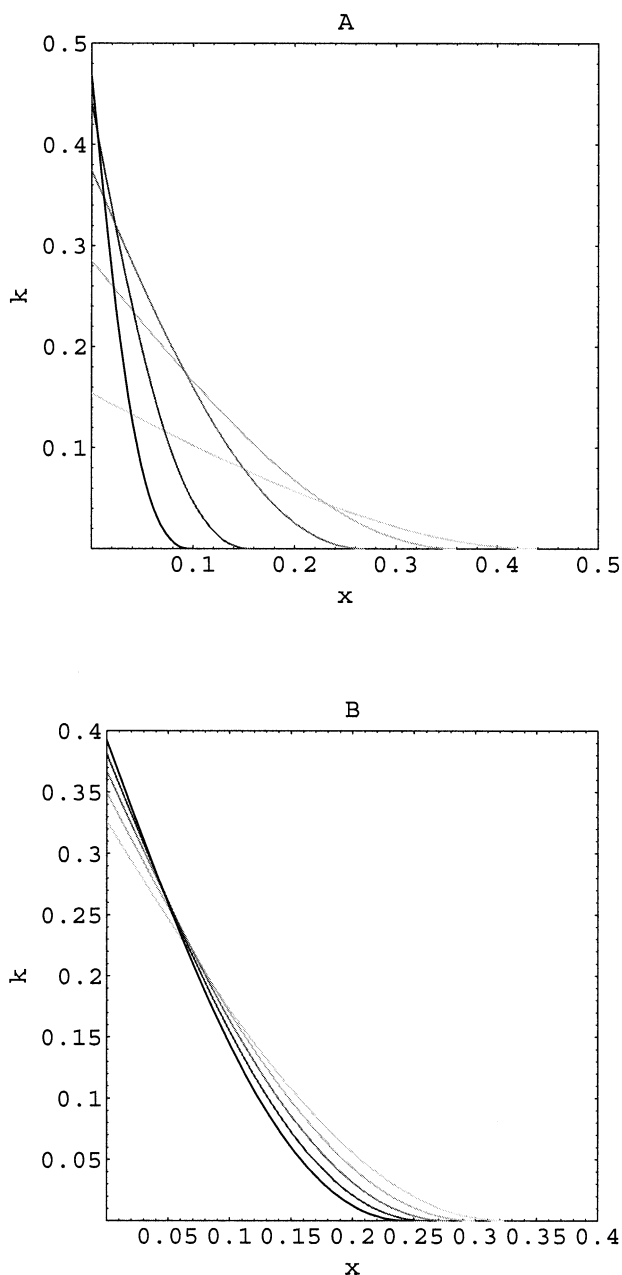
A

Figure 3
The composition of the equilibrium population changes with x (the reduction in competitive ability suffered by conditional strategists). For any given value, the depth of each shaded region corresponds to the frequency of the corresponding type of individual: S indicates sneaks; C(S), conditional individuals that play sneak; C(T), conditional individuals that play territorial; and T, territorials. Other parameter values used to generate this figure were $s = 0.25$, $c = 10$ and $k = 0.1$.

B

Figure 2
Both graphs show the range of conditions under which conditional strategists are able to invade a mixed population of sneaks and territorials, for several different values of c (A) and s (B). Invasion is possible for sufficiently low values of x (the reduction in competitive ability suffered by conditional strategists) and k (the fixed cost suffered by conditional strategists); this is the region below and to the left of the plotted line in each case. In (A), successively darker lines represent successively greater values of c (the ratio of individuals to territories): 2, 5, 10, 25, and 50 (in all cases, $s = 0.25$). In (B), successively darker lines represent successively smaller values of s (the proportion of matings claimed by individuals that play sneak): 0.5, 0.4, 0.3, 0.2, and 0.1 (in all cases, $c = 10$).

Composition of the equilibrium population

The composition of the equilibrium population depends on the limit x (Figure 3). When the limit is very small, the population consists of territorials, conditionals playing territorial and conditionals playing sneak. As the limit increases,
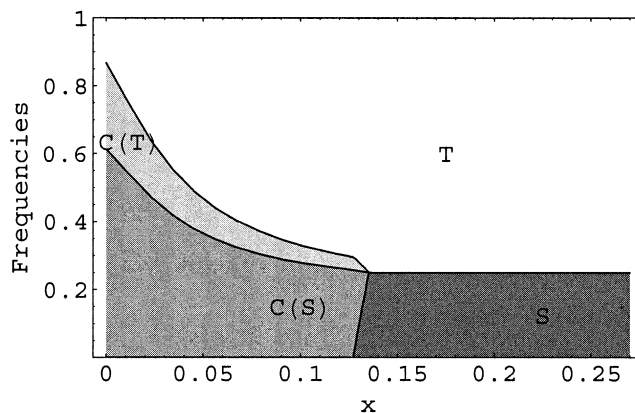
both the total frequency of conditional strategists and the fraction of those conditional strategists that use the territorial tactic decrease, because fewer conditional individuals will have the competitive ability required to successfully hold a territory. At a threshold value of the limit for which the expected fitness of a rare pure sneak is equal to that of a conditional or territorial individual, pure sneaks appear. Past this threshold, the pure sneaks rapidly increase in frequency and conditionals rapidly decrease, because conditionals are rarely holding territories yet are paying a cost relative to pure sneaks. Finally, beyond the point at which conditionals disappear, the proportions of sneaks and territorials remain constant because there are no conditional individuals to be affected by the limit.

How much conditionality?

The model allows for variation in the proportion of conditional individuals in the population, and in the relative frequencies with which conditional individuals adopt sneak and territorial tactics (Figure 3). Clearly, a population in which there is a large proportion of conditional individuals, but in which these conditional types almost always adopt one tactic (sneak or territorial) rather than the other will exhibit little apparent plasticity. Conversely, a population in which there are fewer conditional strategists, but in which these adopt sneak and territorial tactics with similar probabilities, will exhibit greater apparent plasticity. We therefore need an overall measure of conditionality that reflects both the proportion of conditional types in the population, and an observer's uncertainty regarding the tactic that such individuals will adopt (uncertainty reaching a maximum when both sneak and territorial tactics are adopted with equal probability). A suitable measure is

$$U = -f_c[p \log_2 p + (1 - p) \log_2(1 - p)], \qquad (4)$$

where U is the average uncertainty (measured in bits) of an observer regarding the tactic that a randomly chosen individual will adopt, given that its type is known (which ranges from $U = 0$, when $f_C = 0$ or when $p = 0$ or 1, to $U = 1$, when $f_C = 1$ and $p = .5$).
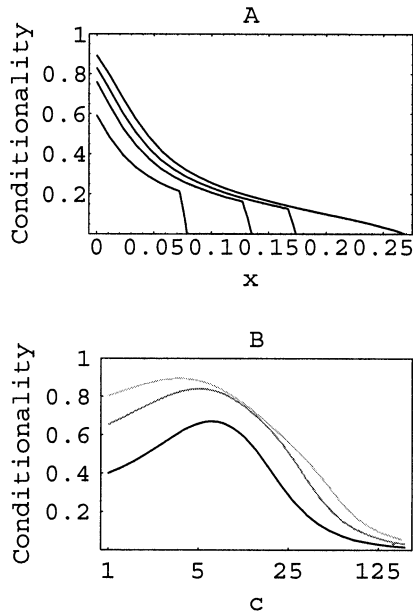
Figure 5
The average number of males contesting each territory at equilibrium, given by $c[f_T + (1 - p)f_c]$ (see Equation A1 in the Appendix), as a function of x, for different values of k. In this case, successively lower curves correspond to successively *lower* values of k: 0.2, 0.1, 0.05, and 0.

Figure 4
(A) shows the equilibrium level of conditionality (average uncertainty, measured in bits, regarding the tactic that a randomly chosen individual will adopt), as a function of x, for several different values of k, when $s = 0.25$ and $c = 10$. Successively lower curves correspond to successively higher values of k: 0, 0.05, 0.1, and 0.2. (B) shows the equilibrium level of conditionality as a function of c, for several different values of s, when $x = k = 0.01$. Successively higher, paler shaded curves correspond to successively higher values of s: 0.1, 0.2, and 0.3.

For a fixed cost (any line in Figure 4a), the average uncertainty decreases as the limit increases, because the frequency of the conditional strategy and the proportion of conditional individuals playing territorial both decline. The rate of decrease in uncertainty becomes much greater at the threshold limit for which pure sneaks are first able to invade (cf. Figure 3). Finally, the uncertainty falls to zero when the conditional strategy disappears, and the tactic adopted by every individual is affected only by its genotype. The higher the cost (successively lower lines on Figure 4a), the lower the frequency of conditional individuals and the lower the uncertainty for any given limit.

The ratio c of males to territories also affects the level of uncertainty (Figure 4b). When c is small, there is little benefit to conditionality because most males seeking a territory are able to obtain one, no matter what their competitive ability. When c is large, there is little benefit to conditionality because only those individuals with the highest competitive ability will obtain a territory, and the existence of a limit means that these individuals are unlikely to be conditional. Thus, the highest level of uncertainty occurs at intermediate values of c. As s increases, the level of uncertainty becomes higher (successively higher lines on Figure 4b). Large s implies a relatively larger gain from sneaking, so there is more benefit to low-conditioned individuals in being able to play sneak. Increasing s also makes the relationship between c and uncertainty less humped. This is because sneaking contributes more to the fitness of the conditional strategy, so the intensity of competition for territories matters less.

How much competition?

Both costs and limits affect the average number of males contesting each territory at equilibrium. For a fixed cost (any
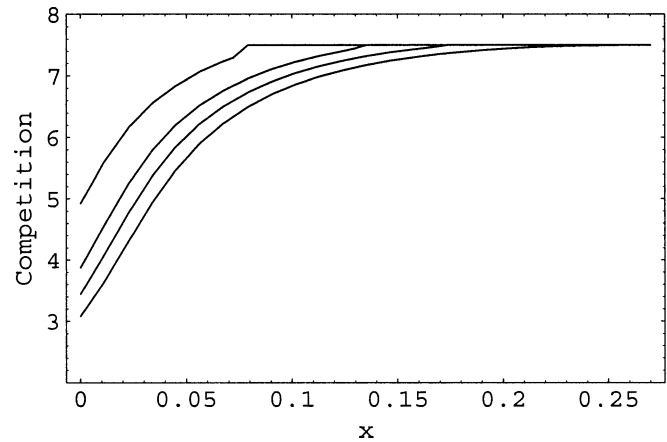
single line in Figure 5), the average number of males contesting each territory increases with increasing limits on the competitive ability of the conditional strategy. This is because the frequency of the pure territorial strategy increases with increasing limits faster than the frequency of conditionals playing territorial decreases. The gradient becomes more steep rapidly at the point at which pure sneaks first appear, then drops to zero when the equilibrium consists only of pure sneaks and territorials. For increasing costs of plasticity (successively higher lines in Figure 5), the frequency of pure territorials increases, so the average number of males contesting each territory is higher. In general, the lower the frequency of the conditional strategy, the higher the level of aggression in the population.

DISCUSSION

It is widely believed that conditional strategies are superior to fixed strategies (Bradshaw, 1965; Scheiner, 1993; Schlichting and Pigliucci, 1998; West-Eberhard, 1989). Previous investigators have acknowledged the possibility of costs and limits associated with conditionality (for reviews, see De Witt et al. 1998, Relyea, 2002), but these have received little attention in the context of alternative mating tactics (but see Moran, 1992). As the present model shows, however, very slight deleterious effects can be sufficient to prevent conditional strategies from entirely replacing fixed strategies. Given our assumption that the strongest competitor always claims a contested territory, an arbitrarily small cost or limit is enough to guarantee that fixed territorial mutants can invade a stable population comprising only conditional strategists.

It is crucial to distinguish between costs that directly reduce the fitness of conditional individuals and limits that reduce the competitive ability or quality that they can attain (De Witt et al. 1998; Relyea, 2002). The effects of both are subtle and qualitatively different. A large enough cost or limit can prevent the invasion of a conditional strategy, but the relative importance of the two depends on the level of mating skew. In general, when mating success is very unevenly distributed, limits on competitive ability are important because only the best quality males are able to obtain territories. When mating success is less dependent on competitive ability, costs that

affect all conditional individuals equally are more important determinants of invasion success. For a given cost and limit, conditional strategies are most likely to be found in populations with intermediate levels of mating skew. They will not be favored when only a very few individuals obtain most of the matings, because conditional individuals are unlikely to achieve the level of quality or competitive ability necessary to obtain a territory. At the other extreme, conditional individuals will not be favored when sneaks obtain almost as many matings as successful territorials, because in this case there is little benefit to being conditional.

At present there are few data on the magnitudes of costs and limits (De Witt et al. 1998; Krebs and Feder, 1997; Nguyen et al., 1989; Relyea, 2002). These can only be measured when there is variation in the level of plasticity within a population (De Witt, 1998; Scheiner and Berrigan, 1998; Van Tiencheren, 1991). For a system with territorial and sneak strategies, such populations have rarely been identified, although our model suggests they may be common. Interpopulation comparative analyses could give some information on costs and limits, although they will suffer from the problems common to all correlational studies.

We know a little more about the level of mating skew in the few systems that appear to be genetic polymorphisms. Many of the most extreme examples of skewed male mating success are found in lek mating systems like that adopted by the ruff, *Philomachus pugnax* (Hill, 1991; Kokko et al., 1999; Mackenzie et al., 1995). Female copying behavior may be a major factor causing this skew (Gibson and Hoglund, 1992; Hoglund et al., 1995; Mackenzie et al., 1995; Wade and Pruett-Jones, 1990). Similarly, in the Japanese damselfly, *Mnais costalis*, there is a high degree of female monopolization (Tsubaki et al., 1997) and females often oviposit on territories in tight aggregated clumps (Plaistow S, personal observations). There are also two three-morph systems that appear to be genetic polymorphisms. Although these are not exactly the case we modeled, they fit the same pattern. The isopod, *Paracerceis sculpta*, has a harem defense mating system with female copying (Shuster and Wade, 1991). In the side-blotched lizard, *Uta stansburiana*, the ultradominant orange-throated male morph maintains large territories with many females (Sinervo et al., 2000). It seems possible that there is the potential for a high degree of within morph mating skew in all these systems, which is consistent with the predictions of our model.

We might expect a relationship between costs or limits and the degree of mating skew. When mating skew is large, there may be strong disruptive selection, resulting in very different phenotypes in the alternative tactics. If it is more difficult to produce two very different phenotypes than to produce two similar phenotypes (e.g., as a result of antagonistic pleiotropy; Moran, 1992), either costs or limits will increase with mating skew.

In the model, territories do not vary in quality, whereas in the real world this is unlikely to be the case. Variability in territory quality may affect the way that mating success is distributed among territory holders, but we do not believe that this will have any effect on the qualitative results of our model. Similarly, we assume that males only contest a single territory. In mating systems in which obtaining a territory is a prerequisite of obtaining mating success disputes over ownership are predicted to be intense, if not fatal. The high cost of fighting means that males often only have a single attempt at getting a territory (see Plaistow and Siva-Jothy, 1996). Nevertheless, even if males can contest more than one territory, this should only have the effect of increasing the average quality of the male that ultimately holds the territory. This effect will occur because multiple contests will reduce the importance of random sampling in determining the rank of the top individual on each territory and will not, therefore, affect the general patterns we observe.

It has usually been assumed that conditional strategies and genetic polymorphisms (featuring two or more fixed strategies) are mutually exclusive evolutionary outcomes (Andersson, 1994). Thus, the existence of some conditional strategists in a population has often been taken as evidence that the whole population consists of conditional strategists (see Gross, 1996). Our model shows that this need not be the case, as equilibria involving territorial and conditional, or sneak, territorial and conditional individuals, are possible (although the three-strategy equilibrium is only stable for a tiny range of conditions). Indeed, we found that a pure conditional equilibrium is only stable if there are neither costs nor limits associated with conditionality. Conversely, cases of apparent genetic polymorphisms may include a conditional strategy in which one of the tactics is only played rarely (which could easily be confused with a weakly heritable fixed strategy). Distinguishing between different types of equilibria may thus be even more difficult than was previously thought.

APPENDIX

Calculating payoffs

The expected payoff to a sneak male is given by Equation 1 in the main text. What about the expected payoffs to territorial and conditional males?

The ratio of competing males (including both fixed territorials and conditional males of high competitive ability) to available territories is equal to

$$c(f_T + (1-p)f_c). \tag{A1}$$

Assuming that males contest randomly chosen territories, the number competing over any given territory will (in a large population) follow a Poisson distribution with mean given by Equation A1. The proportion of territories claimed by at least one male is therefore equal to

$$1 - \text{Exp}[-c(f_T + (1-p)f_c)]. \tag{A2}$$

Each such competition yields a single victor. Hence the proportion of males that compete and are victorious is equal to

$$\frac{1 - \text{Exp}[-c(f_T + (1-p)f_C)]}{c} \tag{A3}$$

and the expected payoff to a successful competitor, denoted v, is thus given by

$$v = \frac{(1-s)c}{1 - \text{Exp}[-c(f_T + (1-p)f_C)]}. \tag{A4}$$

A territorial male will successfully claim its chosen territory if and only if no stronger male contests it. The proportion of males that compete (including both fixed territorials and conditional males of high competitive ability) and are stronger than an individual of quality q, denoted $S(q)$, is given by

$$S(q) = \begin{cases} f_T(1-q) + f_C(1-p), & \text{for } q < (1-x)p \\ f_T(1-q) + f_C\left(\frac{(1-x)-q}{(1-x)}\right), & \text{for } (1-x)p < q < (1-x) \\ f_T(1-q), & \text{for } (1-x) < q \end{cases} \tag{A5}$$

(the three cases in the above expression represent the situation in which [1] the focal individual is weaker than all of the conditional males that become territorial, [2] weaker

than some but not all of such males, and [3] weaker than none of such males).

Assuming again that males contest randomly chosen territories, the number of stronger males competing for a given male's territory follows a Poisson distribution with mean equal to $cS(q)$, where q is the competitive ability of the given male. The probability that the male obtains its territory is given by the zero term of this distribution, $\text{Exp}[-cS(q)]$.

Averaging over all possible competitive abilities, the expected payoff to a fixed territorial individual, w_T, is thus given by

$$w_T = v \int_{q=0}^{q=1} \text{Exp}[-cS(q)]\mathrm{d}q. \tag{A6}$$

In a similar way, we can determine the payoff to a conditional male:

$$w_C = (1-k)\left(p\frac{s}{f_S + pf_C} + v \int_{q=p}^{q=1} \text{Exp}[-cS((1-x)q)]\mathrm{d}q\right) \tag{A7}$$

(the first term in the large brackets covers the possibility of the conditional male becoming a sneak, while the second term covers the possibility of the male becoming territorial).

Searching for solutions

Having calculated the payoffs to the three types of player, we can attempt to determine the equilibrium solution of the model. We begin by considering the conditions under which a mixed equilibrium exists that features only fixed strategies, that is, sneaks and territorials. At such an equilibrium, both types must obtain equal fitness (Bishop and Cannings, 1978). Formally,

$$w_S\big|_{f_C=0} = w_T\big|_{f_C=0}, \tag{A8}$$

which, with Equations 1 and A6, yields the following equilibrium frequencies

$$f_s = s, \qquad f_T = 1 - s \tag{A9}$$

(it is easy to confirm that this is a stable equilibrium, because the fitness of either type is a decreasing function of its frequency in the population).

Under what circumstances can this mixture of sneaks and territorials be invaded by conditional mutants? The payoff to a rare mutant of this kind in the sneak/territorial population is, from Equation A4 and A7, given by

$$(1-k)\left(p + \frac{(e^{cp(1-s)(1-x)} - e^{c(1-s)(1-x)})}{(1-x)(1-e^{c(1-s)})}\right), \tag{A10}$$

where p denotes the probability that the mutant plays sneak. This payoff attains a maximum when p is equal to p_{opt}, given by

$$p_{opt} = \begin{cases} -\left(\frac{cs + \text{Log}\left[\frac{c(1-s)}{e^c - e^{cs}}\right]}{c(1-s)(1-x)}\right) & \text{for } x < \frac{c + \text{Log}\left[\frac{c(1-s)}{e^c - e^{cs}}\right]}{c(1-s)} \\ 1 & \text{for } x > \frac{c + \text{Log}\left[\frac{c(1-s)}{e^c - e^{cs}}\right]}{c(1-s)} \end{cases}. \tag{A11}$$

Comparing the mutant's payoff with that obtained by typical individuals (either sneak or territorial), we find that the population cannot be invaded by a conditional mutant that plays sneak with probability p_{opt} (and by extension cannot be invaded by any other conditional mutant) unless

$$x < \frac{c + \text{Log}\left[\frac{c(1-s)}{e^c - e^{cs}}\right]}{c(1-s)} \tag{A12a}$$

and

$$k < 1 - \frac{1-x}{A}, \quad \text{where } A = \left(\frac{e^{c(1-(1-s)x)}}{e^c - e^{cs}} - \frac{1 + cs + \text{Log}\left[\frac{c(1-s)}{e^c - e^{cs}}\right]}{c(1-s)}\right). \tag{A12b}$$

Equilibria featuring only conditional strategies

We now turn to consider the possibility of an equilibrium at which all individuals adopt a conditional strategy (i.e., $f_C = 1$, $f_S = f_T = 0$). With what probability should individuals at such an equilibrium play sneak? In other words, what is the critical level of standardized competitive ability, p, at which they should switch between tactics? At equilibrium, for an individual of this critical level of competitive ability, both tactics must yield equal fitness. Formally, from Equations 1 through 3 and Equations A1 through A7, we can express this condition as

$$(1-k)\frac{s}{p} = (1-k)\frac{(1-s)ce^{-c(1-p)}}{1-e^{-c(1-p)}}, \tag{A13}$$

where the lefthand side of the above equation gives the expected fitness payoff to an individual of competitive ability p from adopting sneak tactics, and the righthand side the expected payoff from adopting territorial tactics, in a population with members that all switch between tactics at a competitive ability of p. Rearranging, we can express the equilibrium value of p, denoted $\hat{p}$, as

$$\hat{p} = \frac{1}{c}\left[J\left(\frac{s}{(1-s)}e^{c+\frac{s}{(1-s)}}\right) - \frac{s}{(1-s)}\right] \tag{A14}$$

where the function $J(z)$ specifies the real solution for y in $z = y\,e^y$.

It is easy to show that a population of conditional individuals whose switchpoint satisfies Equation A14 is always vulnerable to invasion by a fixed territorial mutant, provided that either x or k (or both) are greater than zero. The payoff to a typical conditional individual in the population is, from Equation A7, given by

$$w_C = (1-k)\left(s + \frac{(1-s)c}{1-e^{-c(1-\hat{p})}}\int_{q=\hat{p}}^{q=1}\text{Exp}[-c(1-q)]\mathrm{d}q\right), \tag{A15}$$

while, from Equation A6, the payoff to a fixed territorial mutant is given by

$$w_T = \frac{(1-s)c}{1-e^{-c(1-\hat{p})}}\int_{q=0}^{q=1}\text{Exp}[-cS(q)]\mathrm{d}q \tag{A16a}$$

$$\begin{aligned} = &\frac{(1-s)c}{1-e^{-c(1-\hat{p})}} \\ &\times \Bigg[\int_{q=0}^{q=(1-x)\hat{p}}\text{Exp}[-c(1-\hat{p})]\mathrm{d}q \\ &+ \int_{q=(1-x)\hat{p}}^{q=(1-x)}\text{Exp}\left[-c\left(1-\frac{q}{(1-x)}\right)\right]\mathrm{d}q \\ &+ \int_{q=(1-x)}^{q=1}1\,\mathrm{d}q\Bigg], \end{aligned} \tag{A16b}$$

which, with Equation A13, yields

$$w_T = \int_{q=0}^{q=(1-x)\hat{p}} \frac{s}{\hat{p}}\mathrm{d}p$$

$$+ \frac{(1-s)c}{1-e^{-c(1-\hat{p})}}$$

$$\times \left[\int_{q=(1-x)\hat{p}}^{q=(1-x)} \mathrm{Exp}\left[-c\left(1-\frac{q}{(1-x)}\right)\right]\mathrm{d}q + \int_{q=(1-x)}^{q=1} 1\,\mathrm{d}q \right]$$

(A17a)

$$= s + \frac{(1-s)c}{1-e^{-c(1-\hat{p})}} \int_{q=(1-x)\hat{p}}^{q=(1-x)} \mathrm{Exp}\left[-c\left(1-\frac{q}{(1-x)}\right)\right]\mathrm{d}q$$

$$+ x(1-s)$$

(A17b)

$$= \frac{w_C}{1-k} + x(1-s),$$

(A17c)

from which it is clear that $w_T > w_C$ (i.e., that the territorial mutant can invade) whenever $k > 0$ or (given that $s < 1$) when $x > 0$. In other words, an arbitrarily small cost or limit associated with conditionality is sufficient to render a purely conditional equilibrium unstable.

It is worth noting that when $k = x = 0$, the expected payoff to a territorial mutant given by Equation A17 is exactly the same as the expected payoff to a typical conditional individual. However, the conditional strategy with switch-point specified by Equation A14 proves stable under these circumstances, because once the territorial mutant type attains a nonnegligible frequency in the population, its expected payoff drops below that of a typical conditional individual.

Equilibria featuring both conditional and fixed strategies

Where neither a purely fixed nor a purely conditional equilibrium exists, we must consider the possibility of a mixed equilibrium featuring sneaks, territorials, and conditional individuals. At such an equilibrium, all three types must obtain equal fitness (Bishop and Cannings, 1978), implying that

$$w_S = w_T = w_C$$ (A17)

In addition, if the conditional individuals in the population play sneak with probability p, the population must be resistant to invasion by conditional mutants that do so with some other probability p' $(\neq p)$. Formally, the payoff to such a mutant, $w_{C'}$, is given by

$$w_{C'} = (1-k)\left(p'\frac{s}{f_S + pf_P} + v \int_{q=p'}^{q=1} \mathrm{Exp}[-cS((1-x)q)]\mathrm{d}q \right),$$

(A18)

and we require that $w_{C'}$ attain a maximum at $p' = p$, which implies that

$$\frac{\partial w_{C'}}{\partial p'} = 0 \quad \text{for } p' = p.$$ (A19)

If Equations A17 and A19 do not yield a meaningful solution (with f_S, f_T, f_C, p all falling between zero and one), we may then turn to consider equilibria featuring a mixture of sneaks and conditional individuals (with no territorials) or a mixture of territorials and conditional individuals (with no sneaks).

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