The unstable dynamics of multiple alternative reproductive tactics

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Abstract

Although negative frequency-dependent fitness is argued to allow the stable coexistence of two alternative reproductive types (such as resource defenders and reproductive parasites), no existing theory has considered a third strategy where resource defenders invest differentially in defence against reproductive parasites. Here, we present the results of a three-strategy game, where reproductive parasites interact with two resource defenders: 'Susceptibles' defend more resources but lose more reproductive success to parasites. 'Immunes' lose less to parasites, but immunity carries a reproductive cost. We show that the inclusion of a third strategy dramatically changes the evolutionary dynamics, such that for a wide range of parameter values, our model predicts the continuous sequential invasion of the three strategies instead of stable coexistence. Our results therefore limit the generality of the prediction that frequency-dependent fitness necessarily allows alternative reproductive tactics to coexist at equilibrium and may also explain the observed dynamics of some multiple-strategy systems.

Introduction

Competition for access to mates or resources is ubiquitous, and extensive research has focused on the evolution of reproductive strategies in the presence of competition among individuals. A commonly observed pattern that has received much attention is the coexistence of alternative reproductive strategies where some individuals invest in resource defence (e.g. territorial or bourgeois tactics) and others parasitize their reproductive efforts (e.g. sneakers or reproductive parasites; Gross & Charnov, 1980; Austad, 1984; Gross, 1984, 1996; Rubenstein, 1984; Shelly & Greenfield, 1989; Shuster, 1989; Rowell & Cade, 1993; Taborsky, 1994, 1997; Lank *et al.*, 1995; Sinervo & Lively, 1996; Henson & Warner, 1997; Alonzo *et al.*, 2000; Jones *et al.*, 2001). Existing theory has clearly demonstrated that negative frequency-dependent fitness can allow the stable coexistence of two alternative reproductive behaviours and that at equilibrium these strategies are predicted to have equal fitness

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(Rubenstein, 1980; Waltz, 1982; Gross, 1984, 1996; Lucas & Howard, 1995; Alonzo & Warner, 2000). Furthermore, extensive empirical research has demonstrated the existence of such alternatives in a number of species, has shown that fitness is negatively frequency-dependent in some of these systems and has attempted, often less successfully, to show that these alternative strategies have equal fitness (Gross & Charnov, 1980; Gross, 1984, 1991; Warner & Lejeune, 1985; Shuster, 1989; Eadie & Fryxell, 1992; Lucas *et al.*, 1996; Sinervo & Lively, 1996; Shuster & Sassaman, 1997; Taborsky, 1997; Widemo, 1998; Andres *et al.*, 2000, 2002; Sinervo *et al.*, 2000; Sinervo & Zamudio, 2001; Brockmann, 2002; Pienaar & Greeff, 2003).

This existing theory has contributed greatly to our understanding of the maintenance of discrete variation within populations. Yet further variation among individuals exists that is not captured by this dichotomous approach. For example, we are not aware of any theory that examines the possibility that individuals exhibit discrete variation in their defence against reproductive parasitism. Imagine, for example, that males defend territories that allow them access to mates or resources important for reproduction. It is conceivable that some individuals may invest in defending a large quantity of

mates or resources, but are consequently more susceptible to reproductive parasites (e.g. 'sneaker' strategies), whereas others focus on defending a smaller quantity of mates or resources and are then more immune to parasitism. Alternatively, individuals can exhibit discrete variation in the type of strategy used to compete for limiting resources or the type of reproductive resource they defend. Assuming there is a tradeoff between the quantity (or quality) of resources defended and the quality of defence against parasitism, we can then ask which strategies are expected to evolve and whether the stable coexistence of alternative reproductive behaviours is possible. Here, we focus on competition for mates or resources important to reproduction. However, similar dynamics could exist for intraspecific brood parasites and their hosts (Eadie & Fryxell, 1992; Nee & May, 1992; Lyon, 1993; Eadie & Lyon, 1998; Ahlund & Andersson, 2001).

Most of the literature on alternative reproductive strategies with respect to resource or territorial defence has either explored interactions between two discrete strategies or examined strategies along a continuum. Yet the empirical observation of more than two discrete alternatives coexisting within a population has created a burgeoning literature on the subject (Sinervo & Lively, 1996; Alonzo et al., 2000; Frean & Abraham, 2001; Kerr et al., 2002; Kirkup & Riley, 2004; Semmann et al., 2004). Interactions between three contestants have the potential to be far more complex than those involving two, and it is well known generally that three-player games can include unstable dynamics relative to two-player interactions, such as in the classic 'rock-paper-scissors' game (Bomze, 1983; Nachbar, 1990; Weissing, 1991; Hofbauer & Sigmund, 1998; Nowak & Sigmund, 2004). One difference between three- and two-strategy games is that interactions between three strategies can involve nontransitive fitness differences. Such nonlinear interactions mean that each strategy can outcompete another strategy but may itself be outcompeted by a third. Biological examples of these complex dynamics have been described for a few systems, most notably the colicin-producing strains of *Escherichia coli* (Kerr et al., 2002; Kirkup & Riley, 2004) and the side-blotched lizard mating system *Uta stansburiana* (Sinervo & Lively, 1996). These systems do not exhibit simple stable coexistence of multiple strategies at equilibrium, but instead exhibit highly complex dynamics related to temporal and spatial variation in the frequency of alternatives (Sinervo & Doughty, 1996; Sinervo & Lively, 1996; Sinervo et al., 2000; Zamudio & Sinervo, 2000; Sinervo & Zamudio, 2001; Calsbeek et al., 2002; Kerr et al., 2002; Sinervo & Clobert, 2003; Svensson et al., 2005).

Here, we consider the specific biological case of three discrete resource defence strategies, in which reproductive parasites attack resource defenders that differ in their ability to defend their resource against reproductive parasites. Susceptible defenders are able to defend a larger amount of resources (or mates) but are parasitized more heavily. In contrast, immune defenders defend a smaller quantity of resources or mates but are more immune to parasites. The extension of classic models examining alternative male reproductive tactics (i.e. resource defenders and reproductive parasites) to include interactions with more than two strategies may seem like a simple mathematical refinement. However, the basis of our theoretical understanding and empirical interpretation of the coexistence of these alternatives is predicated on the idea that, in the presence of reproductive competition, negative frequency-dependent fitness allows the stable coexistence of alternative reproductive strategies with equal fitness. Given that in many biological situations, more than two discrete alternatives may arise biologically, it is important to know whether this basic pattern of stable coexistence persists, as general game theoretical models (e.g. rock-paper-scissors games) clearly show that the stable coexistence of discrete alternatives is often lost when one moves from two to three or more 'players' in a game (Bomze, 1983; Nachbar, 1990; Weissing, 1991; Hofbauer & Sigmund, 1998; Nowak & Sigmund, 2004). We therefore ask, for the specific biological case of reproductive parasites and resource defenders, whether the inclusion of a third strategy alters the basic dynamics and conditions for the coexistence of these alternative reproductive behaviours.

Model description

We use a game theoretical model to explore the evolutionary dynamics, invasion criteria and stability conditions of a reproductive parasite and two alternative resource defence types. We assume that the reproductive parasite and two types of resource defenders are alternative strategies of a single species and that these strategies 'breed true', meaning that their relative fitness determines their relative frequency in or contribution to the next generation (Maynard Smith, 1982; Hofbauer & Sigmund, 1998; Nowak & Sigmund, 2004). The fitness of each strategy in the population is expressed in terms of relative expected reproductive success. In our model, reproductive parasites gain fitness by stealing reproductive resources (which may be mates, fertilizations or other resources important to reproduction) from resource defenders that invest energy in defending those resources. 'Susceptible' resource defenders do not invest as much energy in defending against reproductive parasites and thus lose more resources to parasites than 'immunes' that mount a greater defence against reproductive parasites. Immunes lose fewer resources than susceptibles in the presence of parasites but may also have less time or energy available for reproduction (Moore & Wilson, 2002). For simplicity, we assume that the cost of immunity persists even in the absence of reproductive parasites. Although these tradeoffs may be

viewed in terms of the physiological costs of mounting a defence response (Moore & Wilson, 2002; Blount *et al.*, 2003; Bonneaud *et al.*, 2003; Faivre *et al.*, 2003), we suggest that similar physiological costs may be paid by individuals that spend large amounts of time defending a territory or other resources against reproductive parasitism (von Schantz *et al.*, 1999; Blount *et al.*, 2003; Schwartz & Koella, 2004). Susceptible individuals thus have a fitness advantage in the absence of parasites, and the benefits of immunity depend on the frequency of reproductive parasites.

Let L_S represents the proportion of reproductive success lost on average by a susceptible individual to reproductive parasites and L_I represents the proportion of reproductive success lost on average by an immune individual to parasites. Both L_S and L_I are assumed to depend on the relative frequency of parasites and defenders and are thus functions that increase from zero to some maximum proportion P_S or P_I as the relative frequency of reproductive parasites increases. Consistent with the biology described elsewhere, we also assume that immunes will lose a smaller fraction of their reproductive resources to parasites than susceptibles at the same relative abundance (i.e. $L_I < L_S$ and $P_I < P_S$). Let f_S, f_I, and f_P represent the relative frequency of susceptibles, immunes and parasites in the population, respectively (where $f_S + f_I + f_P = 1$) and n represents the total number of reproductive males in the population overall (such that nf_S, nf_I and nf_P give the number of susceptibles, immunes and parasite males in the population, respectively). Let R_I represents the reproductive capacity (e.g. the ability to obtain reproductive resources or produce viable offspring) of immunes relative to susceptibles in the absence of parasitism (where $R_I < 1$ because we assume immunity carries a cost). The expected relative reproductive success of immunes W_I and susceptibles W_S will depend on both their ability to defend reproductive resources and how much of these resources they lose to reproductive parasites. The relative reproductive success of parasites W_P comes from the reproductive success taken (in the form of resources) from both susceptibles W_{PS} and immunes W_{PI}. The relative fitness of immunes, susceptibles and parasites (W_I, W_S, and W_P) can then be represented as

$$W_S = (1 - L_S) \qquad (1)$$

$$W_I = (1 - L_I)R_I \qquad (2)$$

and

$$W_P = W_{PS} + W_{PI} = L_S\left(\frac{nf_S}{nf_P}\right) + L_I R_I\left(\frac{nf_I}{nf_P}\right) \qquad (3)$$

It is worth noting that the fitness functions above exhibit the following biologically necessary conditions: First, independent of specific values, the total fitness lost by all susceptibles to parasites ($L_S\, n\, f_S$) is equal to the

total fitness gained by all parasites from susceptibles ($W_{PS}\, n\, f_P = L_S\, (n\, f_S/n\, f_P)\, n\, f_P = L_S\, n\, f_S$). Similarly, the total fitness lost by all immunes in the population to parasites ($L_I\, R_I\, n\, f_I$) is equal to the total fitness gained by all parasites from all immunes ($W_{PI}\, n\, f_P = L_I\, R_I\, (n\, f_I/n\, f_P)\, nf_P = L_I\, R_I\, n\, f_I$). In addition, the fitness taken by reproductive parasites from either susceptibles W_{PS} or immunes W_{PI} goes to zero when $nf_S \to 0$ or $nf_I \to 0$, respectively. In addition, the reproductive success that a single rare reproductive parasite (i.e. $f_P = 1/n$) can take from either susceptibles or immunes is bounded such that when $f_P = 1/n$, $W_{PS} = L_S\, n\, f_S$ and $W_{PI} = L_I\, R_I\, n\, f_I$. The three fitness functions depend on the relative frequency of the three strategies because L_S and L_I are functions that depend on the relative frequency of the alternative reproductive behaviours, bounded such that $0 < L_I < P_I < 1$ and $0 < L_S < P_S < 1$ where $P_I < P_S$.

We examine the invasion dynamics, equilibria and stability conditions of the three strategies using standard game theoretical methods and evolutionary invasion analyses (e.g. von Neumann & Morgenstern, 1953; Maynard Smith, 1982; Mesterton-Gibbons, 2001; Diekmann, 2003; Dercole & Rinaldi, 2008). These evolutionary dynamics can be captured by the following discrete-time dynamical system of equations

$$f'_x = \frac{f_x W_x}{f_S W_S + f_I W_I + f_P W_P} \quad (\text{where } x = \text{S, I or P}) \qquad (4)$$

where f'_x represents the frequency of one of the strategies (S, I or P) in the next time period, and the change in frequency of a strategy between generations is given by $\Delta f_x = f'_x - f_x$. A strategy can invade and increase in frequency if $\Delta f_x > 0$ and reaches an equilibrium frequency (f_x^*) when $\Delta f_x > 0$. This frequency (where $\Delta f_x = 0$) will represent a stable equilibrium if $\Delta f_x > 0$ for $f_x < f_x^*$ and $\Delta f_x < 0$ for $f_x < f_x^*$ (locally or globally).

As outlined earlier, we compare the results of the two-strategy game (e.g. only parasites and susceptibles) with the three-strategy game described by the above equations to determine whether the inclusion of the third resource defence strategy alters the basic prediction that negatively frequency-dependent alternatives are predicted to coexist with equal fitness.

Model results and analyses

In the following sections, we describe the invasion criteria, evolutionary dynamics, equilibrium conditions and stability of equilibria for all possible combinations of susceptibles, immunes and parasites (summarized in Table 1).

Parasites with a single type of resource defender

For comparison, we first explore the invasion criteria and coexistence conditions of the game between parasites and a single susceptible host in the absence of immunes

Table 1 Summary of the results of the model. S represents susceptibles, I immunes and P parasites. Invasion is represented by $\rightarrow$ and coexistence by +. 'General case' implies L_S and L_I are increasing functions bounded between zero and P_I or P_S, respectively. 'Specific case' implies L_S and L_I are given by eqns 7 and 9. For the summary below, we assume the following variables are all bounded biologically $0 < R_I < 1$, $0 < P_I < P_S < 1$.

State	General case	Specific case
P only	Never	Never
S only	$L_S < f_P$ (when f_P small)	$P_S < 1/\gamma$
I only	Not stable	Not stable
$I \rightarrow S$	Never	Never
$S \rightarrow I$	Always	Always
$P \rightarrow S$	$L_S \geq f_P$ for f_P small	$P_S \geq 1/\gamma$
$P \rightarrow I$	$L_I \geq f_P$ for f_P small	$P_I \geq 1/\beta$
$S + P$	$f^*_{PS} = L_S$ stable if $L_S > f_P$ for $f_P < f^*_{PS}$ and $L_S < f_P$ for $f_P > f^*_{PS}$ The three-player game further requires $$R_I < \frac{1 - f^*_{PS}}{1 - L_I(f^*_{PS})}$$	As for the general case and also $P_S = \dfrac{f_P}{1 - e^{\left(\frac{\gamma f_P}{f_P - 1}\right)}}$ The three-player game further requires $$R_I < \frac{1 - f^*_{PS}}{1 - P_I} \leq \frac{1 - P_S}{1 - P_I}$$
$I + P$	$f^*_{PI} = L_I$ stable if $L_I > f_P$ for $f_P < f^*_{PI}$ and $L_I < f_P$ for $f_P > f^*_{PI}$ The three-player game further requires $$R_I > \frac{1 - L_S(f^*_{PI})}{1 - f^*_{PI}}$$	As for the general case and also $P_I = \dfrac{f_P}{1 - e^{\left(\frac{\beta f_P}{f_P - 1}\right)}}$ The three-player game further requires $$R_I > \frac{1 - P_S}{1 - f^*_{PI}} \geq \frac{1 - P_S}{1 - P_I}$$
$S + I$	Never	Never
$I \rightarrow S + P$	$R_I < \dfrac{1 - f^*_{PS}}{1 - L_I(f^*_{PS})}$	$R_I > \dfrac{1 - f^*_{PS}}{1 - P_I} \geq \dfrac{1 - P_S}{1 - P_I}$
$S \rightarrow I + P$	$R_I < \dfrac{1 - L_S(f^*_{PI})}{1 - f^*_{PI}}$	$R_I < \dfrac{1 - P_S}{1 - f^*_{PI}} \leq \dfrac{1 - P_S}{1 - P_I}$
$S + I + P$	Never	Never
$S + P \leftrightarrow I + P$	Rarely and only if $$\frac{1 - f^*_{PS}}{1 - L_I(f^*_{PS})} < R_I < \frac{1 - L_S(f^*_{PI})}{1 - f^*_{PI}}$$	Rarely and only by drift if $$R_I = \frac{1 - P_S}{1 - P_I}, f^*_{PS} = P_S \text{ and } f^*_{PI} = P_I$$
Sequential invasion: $S \rightarrow I \rightarrow S + P$	$L_S \geq f_P$ for f_P small and $R_I > \dfrac{1 - f^*_{PS}}{1 - L_I(f^*_{PS})}$ and $L_I = f_P$ not possible	$P_S \geq 1/\gamma$ and $R_I > \dfrac{1 - f^*_{PS}}{1 - P_I} \geq \dfrac{1 - P_S}{1 - P_I}$ and $P_I < 1/\beta$

(i.e. $f_I = 0$, $L_I = 0$). Because reproductive parasites cannot exist without a resource defender to parasitize, the only possible states are a population of all susceptibles (S) or a population of susceptibles and parasites ($S + P$). Applying eqn 4 to the fitness equations above for this two-player game (where $f_I = 0$ and thus $L_I = 0$) yields

$$f'_P = \frac{f_P W_P}{f_S W_S + f_P W_P} = \frac{f_P \frac{L_S f_S}{f_P}}{f_S(1 - L_S) + f_P \frac{L_S f_S}{f_P}} = L_S \quad (5)$$

and

$$f'_S = \frac{f_S W_S}{f_S W_S + f_P W_P} = \frac{f_S(1 - L_S)}{f_S(1 - L_S) + f_P \frac{L_S f_S}{f_P}} = 1 - L_S \quad (6)$$

Parasites can therefore invade susceptibles and increase in frequency whenever $L_S \geq f_P$. Given that $L_S = 0$ must be true when $f_P = 0$, the above implies that parasites will only be able to invade and increase in frequency immunes if $\delta L_S / \delta f_P > 1$ for small values of f_P (Fig. 1). Eqns 5 and 6 also imply that following a successful invasion by parasites, parasites will increase in frequency as long as $L_S \geq f_P$, and parasites will coexist at equilibrium with susceptibles (i.e. not change in frequency) when $f^*_{PS} = L_S$ (which is also where $\delta L_S / \delta f_P = 1$). This gives the biologically sensible result that the relative success of parasites in taking reproductive resources away from susceptibles (L_S) is predicted to determine whether and at what frequency the two alternatives can coexist. For the equilibrium point ($f^*_{PS} = L_S$) of the two-player game to be stable requires $\delta L_S / \delta f_P > 1$ for $f_P < f^*_{PS}$ and $\delta L_S / \delta f_P < 1$ for $f^*_{PS} < f_P$ (Fig. 1).
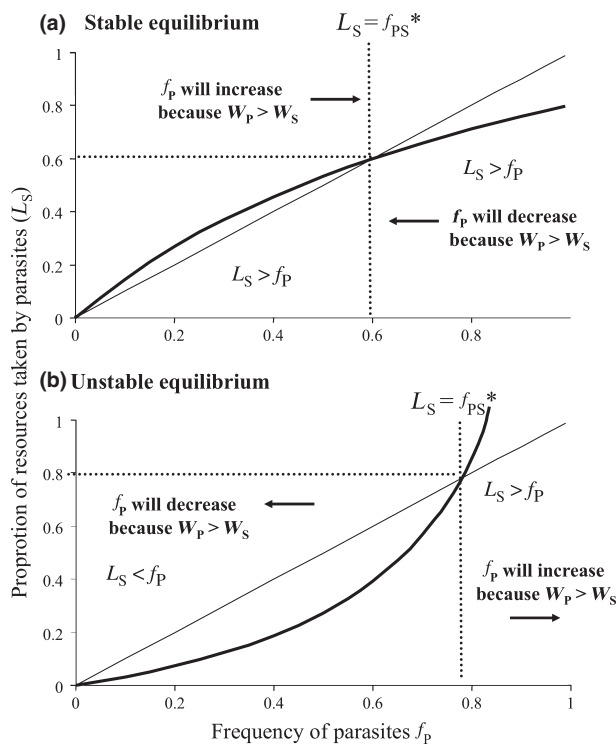
(a) Stable equilibrium

(b) Unstable equilibrium

$$L_S = P_S(1 - e^{-\gamma \frac{nf_P}{nf_S}}) \qquad (7)$$

based on a Poisson distribution, where the constant γ is the efficiency with which parasites take reproductive success away from susceptible hosts and P_S (as above) represents that maximum amount of reproductive success taken (where $0 < P_S < 1$, Fig. 2). This function is undefined for $f_S = 0$ (parasites cannot take fitness from susceptibles if susceptibles do not exist, such that we define that $L_S = 0$ when $f_S = 0$) and bounded between $L_S = 0$ (when $f_P = 0$) and $L_S \rightarrow P_S$ (when $f_P \rightarrow 1$). Given the general invasion dynamics described earlier and the specific function of L_S (eqn 7), parasites can invade susceptibles when $\delta L_S / \delta f_P > 1$ is true for small values of f_P (i.e. when $f_P \rightarrow 0$), which is true for the specific case if

$$P_S > 1/\gamma \qquad (8)$$

This implies that parasites can invade a population of susceptible hosts if the efficiency with which parasites take reproductive success from susceptible hosts (γ) is sufficiently high and the ability of susceptibles to defend themselves against resource parasites is sufficiently low (e.g. P_S sufficiently large that eqn 8 is true).

Unfortunately, when L_S is given by eqn 7, it is not possible to solve analytically for the equilibrium frequency of parasites and susceptibles. However, it is possible to find the strategy frequencies at which $f'_P = f_P$ and $f'_S = f_S$ numerically and graphically (Fig. 3). For the specific relationship represented by eqn 7, a globally stable equilibrium frequency exists whenever parasites can invade (i.e. if $P_S > 1/\gamma$) because $\delta L_S / \delta f_P > 1$ for $L_S < f^*_{PS}$ and $\delta L_S / \delta f_P < 1$ for $L_S < f^*_{PS}$ (as f^*_{PS} occurs where $\delta L_S / \delta f_P = 1$ and $\delta^2 L_S / \delta f_P < 0$ for all biologically relevant values).

In summary, parasites are predicted to be able to invade a single susceptible defender and coexist at a stable equilibrium frequency as long as the proportion of resources that are taken away from individual resource defenders by parasites exhibits a steep relationship at low frequencies of parasites ($L_S > f_P$ for small f_P) and then increases asymptotically with the relative frequency of parasites (f_P / f_S). In general, the two-strategy model predicts that the stable coexistence of reproductive parasites and their hosts will be common.

In the absence of susceptibles, a population of immunes exhibits the same basic conditions for invasion by and coexistence with parasites. Parasites can invade a population of immunes and increase in frequency if $L_I \geq f_P$, and parasites and immunes can coexist at equilibrium where $f^*_{PI} = L_S$ (where the equilibrium frequency of reproductive parasites coexisting with immunes is designated by f^*_{PI}). We consider the same specific functional relationship between L_I and f_P / f_I as we did above for susceptibles such that

$$L_I = P_I(1 - e^{-\beta \frac{nf_P}{nf_I}}) \qquad (9)$$

where P_I is the maximum proportion and β the efficiency with which parasites can take reproductive success from
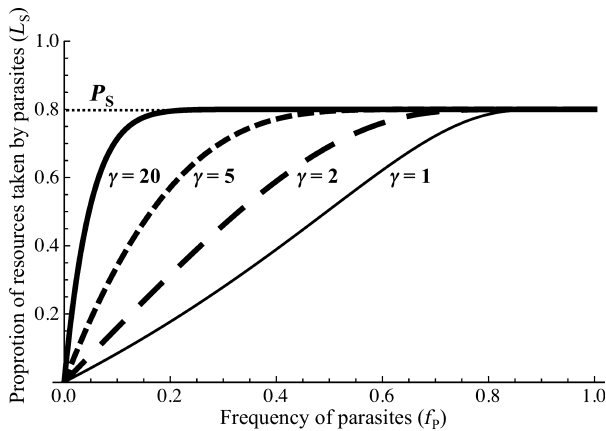
Fig. 1 The frequency-dependent ability of parasites to take reproductive success from resource defenders (L_S) affects the stable coexistence of two alternatives. In both panels, the thick solid line represents L_S as a function of the relative frequency of parasites and the thin line represents unity (e.g. $y = f_P$). Where these two lines cross $L_S = f_P$ and the two alternatives are predicted to have equal fitness on average (in the two-strategy game). The dashed lines represent the values of f_P and L_S at which the two strategies are predicted to have equal fitness. Parasites and resource defenders are only predicted to coexist at equilibrium when L_S increases asymptotically with f_P relative to f_S. (a) The equilibrium point is stable because the frequency of parasites is predicted to return to the stable value following a perturbation. (b) The equilibrium is unstable. See text for details. Similar dynamics apply for immunes and parasites.

The above-described invasion and equilibrium dynamics hold independent of the specific relationship between fitness lost to parasites and the relative frequency of the two alternatives. Biologically, L_S could take on a variety of specific functional forms, depending on the interactions between the alternative strategies and how their relative frequency affects the ability of parasites to take fitness from resource defenders. Here, we examine one explicit function to illustrate the more general dynamics described earlier. However, we fully acknowledge that many other possible forms exist. Imagine that parasites distribute themselves among resource defenders such that each susceptible host will interact with nf_P / nf_S parasites on average. Then, the probability with which parasites successfully take resources from susceptible hosts can be given by the equation

Fig. 2 The effect of the shape parameters γ (or β) on the proportion of reproductive success L_S (or L_I) taken by parasites from individual susceptible (or immune) hosts (for the specific case given by eqns 7 and 9). P_S (or P_I for immunes) represents the maximum proportion of reproductive success that an individual can lose to parasitism.

immune hosts as described earlier for eqn 7 (as above, since eqn 9 is undefined for $f_I = 0$, and we define $L_I = 0$ for $f_I = 0$). Immunes can be invaded by parasites if

$$P_I > 1/\beta \tag{10}$$

As before, it is not possible to find an analytical solution for f_{PI}^*. However, the equilibrium frequency of parasites coexisting with immunes (once they have successfully invaded) will range between 0 and P_I. These are the same basic conditions for invasion and coexistence as found earlier for susceptibles and parasites (summarized in Table 1, Fig. 3). However, immunes are better able to defend themselves against parasites, and parasites are therefore generally predicted to be less common when coexisting with immunes than with susceptibles (i.e. $f_{PI}^* < f_{PS}^*$) and less likely to be able to invade immunes than parasites (because $P_I < P_S$ and $\beta < \gamma$).

Result of the susceptible/immune/parasite game

We now consider the invasion and equilibrium dynamics of all three types simultaneously. Applying eqn 4 to the fitness equations (eqns 1–3) given earlier yields the following set of dynamical equations

$$f_S' = \frac{f_S(1 - L_S)}{f_S + f_I R_I} \quad \text{and} \quad \Delta f_S' = \frac{f_S(1 - L_S)}{f_S + f_I R_I} - f_S \tag{11}$$

$$f_I' = \frac{f_I R_I(1 - L_I)}{f_S + f_I R_I} \quad \text{and} \quad \Delta f_I' = \frac{f_I R_I(1 - L_I)}{f_S + f_I R_I} - f_I \tag{12}$$

$$f_P' = \frac{f_S L_S + f_I R_I L_I}{f_S + f_I R_I} \quad \text{and} \quad \Delta f_P' = \frac{f_S L_S + f_I R_I L_I}{f_S + f_I R_I} - f_P \tag{13}$$

Assuming discrete time and nonoverlapping generations, these three equations capture the dynamics of the
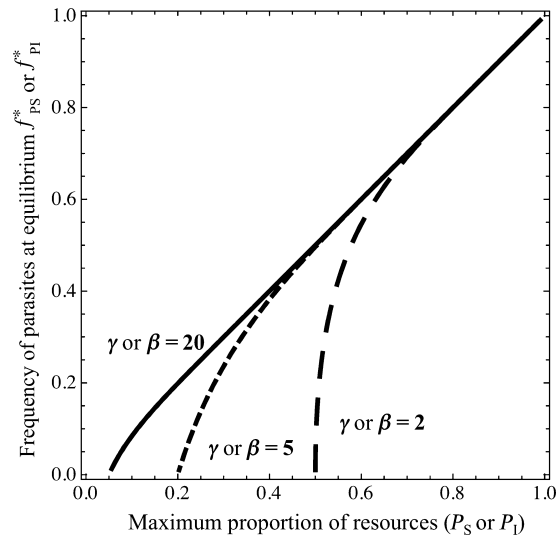

Fig. 3 The frequency of parasites and hosts at equilibrium depends on the ability of hosts to defend themselves against parasites when parasites are common (P_S for susceptibles or P_I for immunes) and the shape of the relationship between the relative frequency of parasites and their ability to take resource from individual hosts (γ or β). In general, for the two-strategy game, reproductive parasites and their resource defending hosts are predicted to coexist at equilibrium if $0 < 1/\gamma < P_S < 1$ or $0 < 1/\beta < P_I < 1$. This is not, however, generally true for the three-player game (see the text and Table 1 for details).

predicted change in frequency for the three strategies. As described earlier, parasites have no fitness in the absence of hosts ($W_{PS} = 0$ if $f_S = 0$ and $W_{PI} = 0$ if $f_I = 0$), and we assume that mounting a greater defence against reproductive parasitism carries an intrinsic cost ($R_I < 1$). In the absence of parasites (i.e. $f_P = 0$) and owing to the costs of immunity, immune hosts can therefore never invade a population of susceptibles and susceptibles can always invade and outcompete a population of immunes. Therefore, four possible stable states exist: susceptibles only (S), parasites and susceptibles ($S + P$), immunes and parasites ($I + P$), or all three strategies ($S + I + P$). We now examine the invasion criteria and equilibria conditions for these four possible states.

The conditions for parasites to invade and increase in frequency in a population of either susceptibles or immunes are the same as in the aforementioned two-strategy case (Table 1). However, we must now also ask whether a population of susceptibles coexisting with parasites will be invaded by immunes and a population of coexisting immunes and parasites can be invaded by susceptibles. For immunes to invade, a population of coexisting susceptibles and parasites requires that $f_I' > 0$ when $f_P = L_S$ and $f_S = 1 - L_S$. Per standard techniques (von Neumann & Morgenstern, 1953), we assume that a rare immune invading a large population of susceptibles and parasites has little effect

on mean fitness of the resident types. A rare immune can therefore invade and increase in frequency (i.e. $\Delta f_{\mathrm{I}} > 0$) if

$$R_{\mathrm{I}} > \frac{1 - L_{\mathrm{S}}}{1 - L_{\mathrm{I}}} \text{ which if } S \text{ and } P \text{ are at equilibrium is}$$
$$R_{\mathrm{I}} > \frac{1 - f_{\mathrm{PS}}^*}{1 - L_{\mathrm{I}}(f_{\mathrm{PS}}^*)} \tag{14}$$

where $L_{\mathrm{I}}(f_{\mathrm{PS}}^*)$ represents the reproductive success lost by a rare immune to reproductive parasites when $f_{\mathrm{P}} = f_{\mathrm{PS}}^*$. The precise dynamics will depend on how fitness lost to parasites depends on the frequency of the two resource defenders relative to the frequency of reproductive parasites. For example, if parasites preferentially associate with susceptibles, immunes could have an advantage when rare (L_{I} small when f_{I} low) and therefore be able to frequently invade and increase in a population of susceptibles and parasites. In contrast, rare immunes (or susceptibles) may be overwhelmed by parasites, in which case the invasion criteria will depend on the maximum fitness loss to parasites (e.g. P_{I}). In general, immunes can invade if the cost of immunity is low (R_{I} large) relative to the loss of fitness to parasites when rare (L_{I}).

For the specific case under consideration, we have made the simplifying assumption that only the relative frequency of parasites affects the fitness lost by a specific resource defender type (see eqns 7 and 9). Given that invading immunes will be rare relative to parasites, we can then infer for this specific case that $f_{\mathrm{P}}/f_{\mathrm{I}}$ will be very large and therefore L_{I} will be equal to its maximum value P_{I}. Though we cannot solve for f_{PS}^* analytically for the specific case, remember that if parasites can invade susceptibles, then $0 < f_{\mathrm{PS}}^* \leq P_{\mathrm{S}}$ (Fig. 3). This means that for the specific case, a rare immune will be able to increase in frequency in a population of susceptibles and parasites at equilibrium if

$$R_{\mathrm{I}} \geq \frac{1 - f_{\mathrm{PS}}^*}{1 - P_{\mathrm{I}}} \geq \frac{1 - P_{\mathrm{S}}}{1 - P_{\mathrm{I}}} \tag{15}$$

Immunes can thus invade a population of susceptibles and parasites at equilibrium if an immune's ability to defend resources (R_{I}) is above a minimum level determined by the efficiency with which parasites take resources away from susceptibles relative to the maximum loss of resources to parasites. If immunes cannot invade (i.e. eqns 14 and 15 do not hold because the cost of immunity is too high), then susceptibles and parasites are predicted to coexist as a stable equilibrium.

We can similarly ask when susceptibles will be able to invade a population of immunes and parasites at equilibrium. This will occur where $W_{\mathrm{S}} \geq W_{\mathrm{P}}$ and $W_{\mathrm{S}} \geq W_{\mathrm{I}}$ when susceptibles are rare. Then, susceptibles will invade for the general case if

$$R_{\mathrm{I}} < \frac{1 - L_{\mathrm{S}}}{1 - L_{\mathrm{I}}} \text{ which if } I \text{ and } P \text{ are at equilibrium is}$$
$$R_{\mathrm{I}} < \frac{1 - L_{\mathrm{S}}(f_{\mathrm{PI}}^*)}{1 - f_{\mathrm{PI}}^*} \tag{16}$$

Again, for the specific case, we can assume that susceptibles will be low in frequency relative to parasites when susceptibles are invading and therefore $f_{\mathrm{P}}/f_{\mathrm{S}}$ will be large, implying that L_{S} will be at its maximum value P_{S}. Given that f_{PI}^* can range between 0 and P_{I}, susceptibles can invade a population of immunes and parasites at equilibrium if

$$R_{\mathrm{I}} \leq \frac{1 - P_{\mathrm{S}}}{1 - f_{\mathrm{PI}}^*} \leq \frac{1 - P_{\mathrm{S}}}{1 - P_{\mathrm{I}}} \tag{17}$$

Thus, there is a maximum value of R_{I} below which susceptibles can invade a population of immunes and parasites. The ability of parasites to take away resources from susceptibles and immunes will determine the minimum cost of immunity that is required for susceptibles to invade immunes and parasites at equilibrium. As described earlier, if susceptibles cannot invade (i.e. eqns 16 and 17 do not hold), then immunes and parasites can coexist as a stable equilibrium.

Parasites (P) can invade and coexist with immunes (I) at equilibrium ($I + P$ possible), and parasites can invade and coexist with susceptibles (S) at equilibrium ($S + P$ possible). We have also determined the conditions for which immunes can invade parasites and susceptibles and the conditions for which susceptibles can invade parasites and immunes (see Table 1). The next relevant question is whether all three strategies can coexist at equilibrium. Through serial solution and substitution, it is possible to show that coexistence is not possible for biologically feasible parameter values independent of the precise functional form of frequency-dependent fitness loss to reproductive parasites (i.e. L_{S} and L_{I}). Given that we are interested in the coexistence of all three types, we are only interested in solutions where $0 < f_{\mathrm{S}}, f_{\mathrm{P}}$ and $f_{\mathrm{I}} < 1$ (and $f_{\mathrm{S}} + f_{\mathrm{P}} + f_{\mathrm{I}} = 1$). The stable coexistence of the three alternative reproductive strategies requires that $\Delta f_{\mathrm{S}} = \Delta f_{\mathrm{I}} = \Delta f_{\mathrm{P}} = 0$. Solving eqn 12 for f_{S} when $\Delta f_{\mathrm{I}} = 0$ gives $f_{\mathrm{S}} = R_{\mathrm{I}}(1 - f_{\mathrm{I}} - L_{\mathrm{I}})$. Substituting for f_{S} into eqn 13 and solving for f_{I} when $\Delta f_{\mathrm{P}} = 0$ yield $f_{\mathrm{I}} = 1 - L_{\mathrm{I}}$. By further substituting for f_{I} and f_{S} into the equation given above for f_{S} and for $f_{\mathrm{S}} = 1 - f_{\mathrm{P}} - f_{\mathrm{I}}$ yields $f_{\mathrm{S}} = 0$, thus demonstrating that stable coexistence of all three types is not possible.

Given that the three alternatives cannot coexist as a stable equilibrium, we can then ask whether the sequential invasion of strategies is possible. For example, given that the stable coexistence of parasites and a single host is possible ($S + P$ and $I + P$), is it possible to alternate between these two states as alternative hosts invade and outcompete the other host? This would require conditions allowing immunes to invade a population of

susceptibles and parasites at equilibrium and parasites to invade a population of immunes and parasites at equilibrium. These conditions for invasion are given for the general case (by eqns 14 and 16) and the specific case (by eqns 15 and 17, Table 1) above. For this type of sequential invasion ($S \rightarrow I + P$ and $I \rightarrow S + P$), the following must be true in general

$$\frac{1 - f_{PS}^*}{1 - L_I(f_{PS}^*)} < R_I < \frac{1 - L_S(f_{PI}^*)}{1 - f_{PI}^*} \tag{18}$$

Given that $0 < R_I < 1$ and $f_{PI}^* < f_{PS}^*$, eqn 18 implies that sequential invasion will arise only if the cost of immunity is balanced by its benefits in terms of avoiding fitness lost (e.g. R_I falls between the relative fitness loss ratios given above). For the specific case, eqns 16 and 17 imply that sequential invasion would only occur by drift and further requires that

$$R_I = \frac{1 - P_S}{1 - P_I} \text{ and } f_{PS}^* = P_S \text{ and } f_{PI}^* = P_I \tag{19}$$

Only for these specific (and rather extreme) parameter conditions would the fitness of immunes and susceptibles be equal to the resident resource defenders, which might allow mutant resource defence strategies to increase in the population by drift. However, this situation is only possible in the very special (and unlikely) case where the cost of immunity is exactly balanced by a decrease in fitness lost to parasites and parasites are very efficient at taking reproductive success from resource defenders (β and γ large, which in essence makes the fitness of the two resource defenders have equal fitness across a wide range of parasite frequencies and thus able to drift between $f_P = P_I$ and $f_P = P_S$). Otherwise, it is not possible for alternative hosts to sequentially invade one another as they coexist with parasites. Instead, when both immunes and susceptibles can be invaded by and coexist with parasites, either immunes with parasites or susceptibles with parasites will represent a globally stable equilibrium. Which combination of the two will persist depends on which resource defender has the fitness advantage and can invade the other in the presence of reproductive parasites (Table 1, Fig. 4a,b).

We have seen that all three strategies are not predicted to coexist, that single hosts (immunes or susceptible) can coexist with parasites, but that stable oscillations between parasitized immunes and susceptible are not expected (Table 1). However, a final possibility exists: the sequential invasion of all three strategies (e.g. alternation between $S \rightarrow I \rightarrow S + P \geq I$). This would arise if parasites can invade a population of susceptibles but cannot invade a population of immunes. Biologically, this represents the existence of a tradeoff between high levels of resource defence (susceptibles) and successful defence against reproductive parasites (immunes). As described earlier (and summarized in Table 1), this will require that parasites can invade and coexist with susceptibles, which is possible if
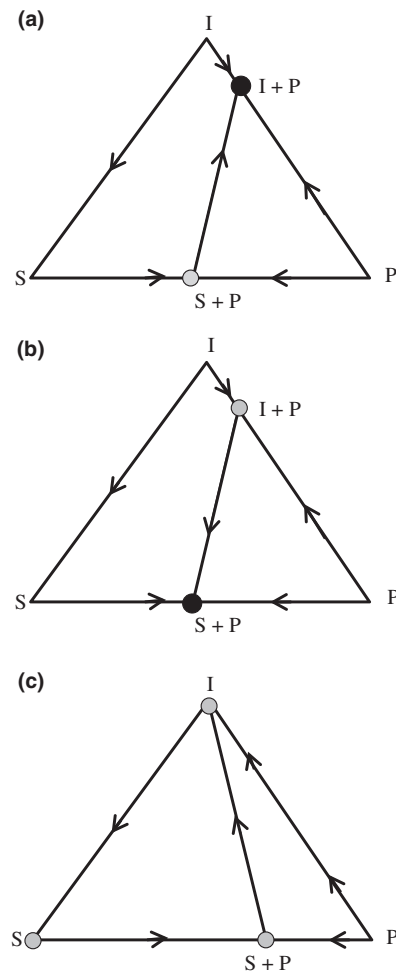

Fig. 4 The potentially unstable dynamics of alternative reproductive strategies. (a) Immunes and parasites ($I + P$, back dot) can represent a global equilibrium, if immunes can invade a population of coexisting susceptibles and parasites ($I \rightarrow S + P$) but can also be invaded by and coexist with parasites ($P \rightarrow I$). (b) Susceptibles and parasites ($S + P$, back dot) can represent a globally stable equilibrium, if susceptibles can invade a population of coexisting immunes and parasites ($S \rightarrow I + P$) but cannot then be invaded by immunes. (c) No stable equilibrium exists if immunes can invade coexisting susceptibles and parasites but cannot themselves be invaded by parasites. Instead, the sequential invasion of strategies is predicted changing from only susceptibles (S) to susceptibles and parasites ($S + P$) to all immunes (I) and back to susceptibles again (S, possible states shown as grey dots). For all three panels, the predicted change in the frequency of the three strategies is shown using a De Finetti diagram where each point within the triangle represents a different combination of the frequencies of each strategy as follows: the frequency of immunes f_I changes from 0 to 1 moving from base to the apex labelled I, the frequency of parasites f_P changes from 0 to 1 moving from the left vertex to the right corner (labelled P), and the frequency of susceptibles f_S changes from 0 to 1 moving from the right vertex to the left corner (labelled S). Arrows show the predicted direction of change in strategy frequencies. Invasion, equilibria and stability criteria are summarized in Table 1 and described in the text.

$$1/\gamma < P_S \qquad (20)$$

and immunes can invade and outcompete a population of susceptible and parasites when

$$R_I \geq \frac{1 - f_{PS}^*}{1 - P_I} \qquad (21)$$

and yet immunes cannot be invaded by parasites if (but instead will go to fixation)

$$P_S < 1/\beta \qquad (22)$$

When these conditions are all met (given by eqns 20–22), the sequential invasion and alternation between three states is predicted (immunes alone, susceptibles alone, and susceptibles and parasites, see Fig. 4c) and the globally stable coexistence of any one or two strategies is not predicted (despite the existence of negative frequency-dependent reproductive success). It should also be pointed out that a wide range of biologically reasonable parameter combinations allow these conditions to be met.

Discussion

For this biological scenario, all three strategies are never predicted to coexist in the same population with equal fitness. Whereas for some parameter combinations, either immunes or susceptibles will coexist with reproductive parasites (e.g. two alternatives will exist at equilibrium, Fig. 4a,b), there are also many conditions in which coexisting susceptibles and parasites can be invaded and outcompeted by immunes, which are then invaded by susceptibles, which are then invaded by reproductive parasites (Fig. 4c). By contrast, the two-strategy game with identical fitness equations and parameter values predicted the stable coexistence of two alternatives. The stable coexistence of a single resource defence strategy and parasites is only predicted when immunity is either very costly relative to its benefits (where susceptibles and parasites are predicted to coexist) or very easy to obtain (where immunes and parasites are predicted to coexist). However, as long as there is a reasonable tradeoff between the costs and benefits of immunity, the sequential invasion of all three strategies is predicted and no single strategy or combination of strategies is globally stable (Table 1, Fig. 4). Clearly, the inclusion of a third strategy (an alternative resource defender) alters the basic predictions and expected dynamics of the classic interaction between reproductive parasites and resource defenders. As such, we suggest that interesting biological interactions may be missed if the possibility of more than two alternatives is not considered in theory and identified in the wild.

In this paper, we have focused on comparing the dynamics of the classic two-strategy game between reproductive parasites and their resource defending hosts with a three-strategy game that includes two types of hosts. As described previously, our results clearly indicate

that the model predictions are greatly altered by the inclusion of a third strategy. But what does this imply biologically? We can make the following general predictions. First of all, if a single 'best' resource defence strategy does not exist, there will be cases in which we will not observe the stable coexistence of two alternatives, even though we might expect them based on the existence of negative frequency-dependent fitness. One might also observe spatial and temporal variation in the frequency and fitness of alternatives. However, this pattern does not necessarily imply that the frequency-dependence of fitness is changing over space or time. Instead, the unstable dynamics of multiple alternatives alone can explain temporal and spatial variation in the frequency and occurrence of alternative reproductive behaviours. It is also possible that meta-population dynamics (where individuals move among spatially distinct subpopulations) could maintain all multiple alternatives at a large spatial scale as individual demes cycle in frequency. Empirically, this implies that we should look for spatial and temporal variation in the fitness and frequency of alternatives (Sinervo & Lively, 1996; Kerr *et al.*, 2002; Kirkup & Riley, 2004; Svensson *et al.*, 2005) and that we need to consider the possibility that alternatives are not simply dichotomous (e.g. that variation exists within a strategy 'type'). Recent empirical work suggests that our theoretical results are broadly supported in nature. Corl *et al.* (2010) demonstrated, in a broad biogeographical survey of the side-blotched lizard's throat colour polymorphism (Sinervo & Lively, 1996), the repeated loss of one throat colour morph in independent populations of lizards. Specifically, the yellow-throated 'sneaker' morph (i.e. analogous to the reproductive parasite described here) has been lost in at least eight separate events, suggesting a dynamic history of unstable morph coexistence.

Our results clearly indicate that discrete variation in resource defence strategies can destabilize the coexistence of negatively frequency-dependent alternatives. However, more theory is clearly needed to determine the generality of this pattern. The inclusion of more than three alternatives may further alter the dynamics. Continuous variation in a variety of reproductive strategies rather than discrete alternatives should also be considered in the future. Whereas the precise patterns of stability and coexistence may depend on the specifics of the model, our results clearly indicate that it is incorrect to assume that the stable coexistence of two alternatives is generally predicted in the presence of negative frequency dependence. Instead, an understanding of the presence or absence of alternative reproductive strategies (such as sneakers and territorial males) requires considering whether more than two alternatives may be possible even if they are not observed simultaneously within a population.

Past research has clearly demonstrated the existence of alternative reproductive behaviours in a variety of

species and, in some cases, it has been documented that they exhibit negative frequency-dependent fitness. Clearly, it is possible for reproductive parasites and resource defenders to coexist. However, our model demonstrates that the possibility of alternative resource defence (host) strategies can destabilize the classic coexistence predicted by two-strategy models. We do not wish to argue that alternatives may not be maintained by frequency dependence. However, we believe that it is important to consider the existence of multiple strategies within a population and argue that the complex and apparently unstable dynamics exhibited by some of the well-studied examples of three strategy systems (Sinervo & Lively, 1996; Kerr et al., 2002; Kirkup & Riley, 2004; Svensson et al., 2005; Corl et al., 2010) may be explained generally by the dynamics we report here. Our results indicate that if we wish to fully understand the maintenance of discrete variation within populations, we need to allow for more than two alternative behaviours within a population and focus on documenting spatial and temporal variation in the frequency and fitness of alternatives. Although negative frequency-dependent fitness can maintain two alternative reproductive behaviours, species in which we do not observe the classic expectation of two alternatives with equal fitness may be explained by the consideration of the unstable dynamics of multiple alternative reproductive tactics.

Acknowledgments

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