

Cheating can stabilize cooperation in mutualisms

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Mutualisms present a challenge for evolutionary theory. How is cooperation maintained in the face of selection for selfishness and cheating? Both theory and data suggest that partner choice, where one species preferentially directs aid to the more cooperative members of the other species, is central to cooperation in many mutualisms. However, the theory has only so far considered the evolutionary effects of partner choice on one of the species in a mutualism in isolation. Here, we investigate the co-evolution of cooperation and choice in a choosy host and its symbiont. Our model reveals that even though choice and cooperation may be initially selected, it will often be unstable. This is because choice reduces variation in the symbiont and, therefore, tends to remove the selective incentive for its own maintenance (a scenario paralleled in the lek paradox in female choice and policing in within-species cooperation). However, we also show that when variability is reintroduced into symbionts each generation, in the form of less cooperative individuals, choice is maintained. This suggests that the presence of cheaters and cheater species in many mutualisms is central to the maintenance of partner choice and, paradoxically, cooperation itself.

Keywords: mutualism; partner-choice; sanctions; cheating; cooperation; lek paradox

1. INTRODUCTION

The evolution of cooperation between species (mutualism) poses a problem for evolutionary theory (Herre *et al.* 1999; Bronstein 2003; Sachs *et al.* 2004; Foster & Wenseleers *in press*). Natural selection will favour any cheater that can receive the benefits of mutualism without providing anything in return. What then prevents cheaters from undermining the myriad of mutualisms that we see in nature?

A number of mechanisms that limit selection for cheating in mutualisms have been identified (reviewed in Sachs *et al.* 2004; Foster & Wenseleers *in press*). As expected, all these mechanisms tie mutualistic investment in a partner species to personal fitness. Most simply, mutualism may occur because it has a direct fitness benefits (by-product effects, Connor 1986; Connor 1995; Sachs *et al.* 2004), such as a bacteria species releasing a waste product that benefits another species. However, in many systems, there will also be feedback benefits to cooperation through its effects on a partner species (Foster & Wenseleers *in press*). Three main feedbacks have been discussed. First, being mutualistic may mean that an individual tends to associate with the more cooperative genotypes of the other species (*cooperator association*, Frank 1994; Doebeli & Knowlton 1998; Wilkinson & Sherratt 2001; Yamamura *et al.* 2004). Second, when mutualism improves the fitness of a partner species, this may improve its phenotypic ability to return aid

(*partner-fidelity feedback*, Bull & Rice 1991; Sachs *et al.* 2004). Finally, the partner species may have a specific behavioural adaptation that preferentially directs aid to more mutualistic individuals (*partner choice and sanctions*, Bull & Rice 1991; Noe & Hammerstein 1994; Johnstone & Bshary 2002; West *et al.* 2002a,b; Sachs *et al.* 2004).

Feedbacks through a partner species will only favour mutualism, however, when a significant amount of the feedback benefit returns to the individual that initiated the feedback or their relatives. Therefore, within-species relatedness and between-species fidelity must both be high at the scale of the feedback (Foster & Wenseleers *in press*). That is, effects on a mutualist partner that feedback on the whole population (low relatedness) or only return after an individual has left the group (low fidelity) will not select for mutualism. This suggests that rapid phenotypic effects from partner-fidelity feedback and partner choice are central to the evolution of mutualisms. In particular, theory suggests that partner choice, being behavioural and hence local and rapid in effect, can strongly select for between-species cooperation (Bull & Rice 1991; Noe & Hammerstein 1994; Ferriere *et al.* 2002; Johnstone & Bshary 2002; West *et al.* 2002b; Sachs *et al.* 2004; Foster & Wenseleers *in press*). In support of this, a large body of empirical data is emerging that suggests that partner choice mechanisms are widespread and common in many mutualisms (Sachs *et al.* 2004; Foster & Wenseleers *in press*).

It is clear then that partner choice can select for cooperation and mutualism, but what about the evolution of choice itself? West *et al.* (2002a) modelled the mutualism between legumes and rhizobial bacteria, where the legumes provide photosynthate and, in return, receive fixed nitrogen from the bacteria. The model predicted that legumes could benefit from preferentially directing resources towards more cooperative rhizobia in

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Table 1. Summary of the main notations.

| notation | description |
|-----------|--|
| a | genetically determined investment in cooperation (species A) |
| b | genetically determined investment in cooperation (species B) |
| c | genetically determined investment in partner choice (species A) |
| f | weighting determining cost of partner choice to species B (affects species A indirectly) |
| g | weighting determining direct cost of partner choice to species A |
| $H(a, c)$ | probability density of species A individuals with cooperation level a and choice level c |
| $S(b)$ | probability density of species B individuals with cooperation level b |
| m | immigration from source population each generation (as a proportion of focal population) |
| p | effect of partner-fidelity feedback |
| q | effect of partner choice by species A on species B |
| s | weighting determining mutation rate to reduced cooperation in species B |
| W | fitness of focal individual |
| x | weighting determining benefit to species A of receiving mutual aid from B |
| y | weighting determining benefit to species B of receiving mutual aid from A |

their roots, even when this comes at a cost and reduces the overall number of bacteria. Previous work has shown, therefore, that partner choice can be selected and that choice can promote cooperation. However, to date, no study has looked at how cooperation and choice coevolve in mutualistic partners. We developed a model to investigate this question based upon a host–symbiont mutualism. Importantly, our model predicts that even though choice and cooperation may be initially selected, it will often be unstable. This is because choice reduces variation in the symbiont and, therefore, tends to remove the selective incentive for its own maintenance. However, we also show that partner choice can be maintained when variability is reintroduced into the symbionts each generation. Our findings have an interesting parallel in the lek paradox of sexual selection, where a source of variability in males is required to explain the maintenance of female choice (Kirkpatrick & Ryan 1991; Tomkins *et al.* 2004).

2. THE MODEL

The model is based upon two species that can benefit from helping one another, where one species may also perform partner choice: preferential association with, or provision of mutual aid to, the more cooperative members of the other species. This is consistent with a wide variety of mutualism in which partner choice occurs, but is only present in one of the two partner species (Sachs *et al.* 2004; Foster & Wenseleers *in press*). Our central question is: when will stable cooperation evolve in this system?

For illustrative purposes, our model is phrased in terms of a host/symbiont system such as plants with rhizobial bacteria (West *et al.* 2002a,b; Kiers *et al.* 2003; Simms *et al.* 2006) or mycorrhiza (Strack *et al.* 2003) living on or in their roots, jellyfish with photosynthetic algae (Sachs & Wilcox 2006), or the light emitting bacterium *Vibrio fischeri* that lives in the light organ of the bobtail squid (Visick *et al.* 2000). However, the key conclusions of the model are likely to equally apply to all mutualisms where partner choice can occur, such as cleaner fish and their clients (Grutter 1999; Bshary & Grutter 2002), and pollinators and plants (Pellmyr &

Huth 1994; Smithson & Gigord 2003). Like West *et al.* (2002a), we consider the case where many unrelated strains of symbiont occur in each host because partner choice will have no evolutionary effect on symbionts when they are a single clone and no choice can be made. We calculate the fitness of two mutualist species (W_A , W_B) using two central equations (table 1; Foster & Wenseleers *in press*),

$$W_A = (1 - a) + xp_A \bar{b}(c) - gc, \quad (2.1)$$

$$W_B = (1 - b) + yp_B aq(b, c). \quad (2.2)$$

Here, a and b are the genetically determined investment in cooperation by a host (species A, $0 \leq a \leq 1$) and a symbiont (species B, $0 \leq b \leq 1$) individual, respectively, and $\bar{b}(c)$ is the mean level of cooperation in the symbiont group (for a given level of partner choice c , as choice can exclude uncooperative individuals, see below). The weighting terms x and y determine the benefit to each species of receiving aid from the other. For example, x will be large if a small amount of nitrogen from rhizobia greatly benefits a host plant.

We assume that the host species (A) can engage in partner choice, c . The effect of c on the symbiont (species B), is represented by $q(b, c)$ in equation (2.2) and it can be interpreted as a propensity of the host to accept the symbiont for continued interaction, or, equally, as the proportion of total mutualistic aid directed to a symbiont with a given level of cooperation. We assume $q(b, c)$ increases with b and c , such that B's fitness increases more sharply with its cooperation b if A is more choosy (i.e. $\partial^2 q / \partial b \partial c > 0$, below). The host species A, however, also suffers a direct cost of being choosy; gc in equation (2.1) is the energetic cost to species A from exercising choice, g expressing the marginal cost. Finally, providing aid to a mutualist species will, in many cases, affect their phenotype by increasing their numbers, health, size or survival. This may feedback on the focal individual as increased return aid. We capture such 'partner-fidelity feedback' (Sachs *et al.* 2004; Foster & Wenseleers *in press*) with p_A and p_B , which are a positive function of the level of cooperation of a focal species (see equations (2.5) and (2.6)). In the following sections, we expand and further define a number of the terms in these equations.

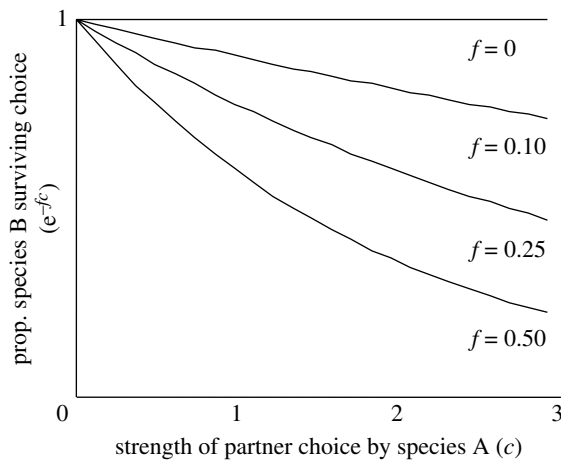


Figure 1. The effect of partner choice by the species A on species B, for various values of the weighting parameter f (equation (2.3)).

(a) Partner choice

The effect of partner choice on a focal symbiont with cooperation level b can be written as:

$$q(b, c) = \frac{e^{bc}}{\int_0^1 e^{bc} S(b) db} e^{-fc}. \quad (2.3)$$

Here, $q(b, c)$ is the effect of choice on the fitness of the symbiont (species B), and c is the strength of choice by the host species A. An exponential form allows the model to include possibly strong relationships between cooperation and fitness returns, despite a limited range of b and c . $S(b)$ is the probability density of symbionts with a cooperativity of b , which is determined by the frequency of symbionts of each level of cooperation that interact with the host. The denominator term makes the effect of host choice on the focal symbiont relative to the cooperation of the other symbionts interacting with the host. Choice may also reduce the total number or fitness of the symbionts. We allow for this possibility by introducing the term f , which defines a negative relationship between choice strength and its effect on all symbionts over all levels of cooperation (figure 1). Note that this will feedback as a cost to the host, in addition to any direct energetic cost that the host experiences from choice (g , equation (2.1)).

Partner choice results in discrimination against uncooperative symbionts. This influences the mean cooperativity in a symbiont group by increasing the frequency of the more cooperative symbionts relative to the less cooperative ones. Mean cooperativity after choice ($\bar{b}(c)$) can be written as,

$$\bar{b}(c) = \frac{\int_0^1 q(b, c) S(b) b db}{\int_0^1 q(b, c) S(b) db}. \quad (2.4)$$

(b) Partner-fidelity feedback

As in most models of mutualism (Frank 1994; Doebeli & Knowlton 1998; West *et al.* 2002b; Foster & Wenseleers in press), we include a partner-fidelity feedback effect, where mutualistic aid by one species increases the ability of the other species to return aid. This might occur, for example, if host investment in mutualism is proportional to symbiont abundance and, therefore, the level of mutual aid returned by the symbionts. For a host, this gives:

$$p_A = ay. \quad (2.5)$$

For a focal symbiont, partner-fidelity feedback from the host will depend on the mean cooperativity of all symbionts interacting with its host,

$$p_B(c) = \bar{b}(c)x. \quad (2.6)$$

(c) Final model

We can use the above derivations to expand equation (2.2) for the fitness of the symbionts. In order to do this, we calculate average symbiont fitness across all possible hosts because each symbiont's genotype will, on average, experience the full range of hosts in the population that possess different levels of cooperation a and choice c (we assume complete mixing each generation so there is no cooperator association, Frank 1994; Foster & Wenseleers in press). Fitness of a focal symbiont of cooperation level b is therefore:

$$W_B = (1-b) + y \int_0^1 \int_0^{c_{\max}} H(a, c) q(b, c) p_B(c) a dc da, \quad (2.7)$$

where c_{\max} denotes the strongest possible choice. The double integral calculates the mean mutualistic benefit provided across all hosts in the population, where $H(a, c)$ is the probability density of species A hosts with cooperation level a and choice level c .

(d) The simulation

We followed the evolution of cooperation and choice in species A (a, c) and cooperation in species B (b) across generations using a simulation. We chose to use a simulation because it allowed us to avoid restrictive assumptions such as weak selection or normal distributions around mean values of traits, and to investigate the sometimes-complex interaction between the three variables. These interactions include the inter-dependency of selection for partner choice in A and variability in cooperativity in B (below, figure 2b), which is difficult to capture analytically. The simulation was performed in MATLAB (MathWorks, Inc.) and based upon a discretized matrix for each species that defined the proportion of individuals of each level of cooperation (a, b) and, for species A, also choice (c). For the simulations shown, species A was represented with an 11×11 matrix with one axis as cooperation (a , range 0 ... 1) and the other as choice (c , range 0 ... 3). Increasing the upper bound for choice $c_{\max} > 3$ had little effect on the simulation because individuals very rarely evolved to reach this value (figure 2). Species B had an 11×1 vector that defined the proportion of individuals at each level of cooperation (b , range 0 ... 1). Additional simulations with finer matrices produced consistent results and suggested that our conclusions were not an artefact of the relatively few categories in the matrices of the main simulations.

Numerical approximations of equations (2.1) and (2.7) gave the fitness associated with each position in the matrices each generation, which in turn, enabled the frequencies in the next generation to be calculated. Note that this procedure allows for genetic covariances to develop between cooperation and choice in species A, which can be important for coevolving traits (Gardner & West 2004): e.g. selection can remove individuals that have a high a combined with a low c , should these be unsuccessful. In our simulations, a positive covariance between cooperation and choice was sometimes seen in

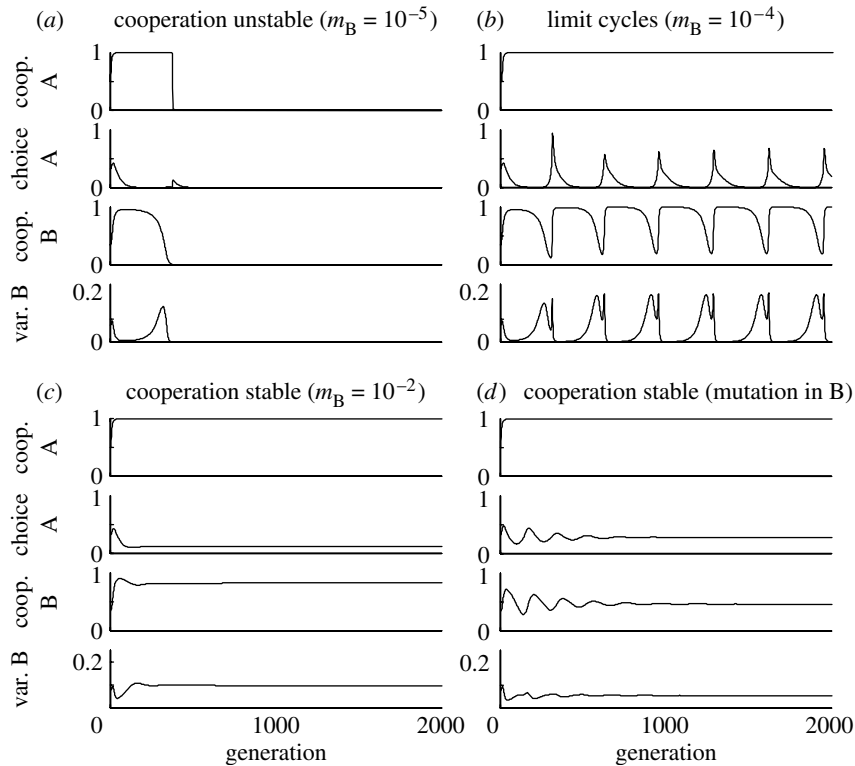


Figure 2. Mutualism that is initially selected is not always stable. The four simulations illustrate the range of outcomes when partner choice carries a cost ($f=0.1$, $g=0.1$). (a) Cooperation unstable. Immigration from source population: $m_B=10^{-5}$. (b) Limit cycles, $m_B=10^{-4}$. (c) Cooperation stable, $m_B=10^{-2}$. (d) Cooperation stable: this simulation assumes biased mutation in species B towards less cooperation each generation, $s=0.1$. Axes are ‘coop. A’, mean level of cooperation in species A (\bar{a}); ‘choice A’, mean level of partner choice in species A (\bar{c}); ‘coop. B’, mean level of cooperation in species B (\bar{b}); ‘var. B’, variance in cooperation in species B. Unless stated parameters in the simulations are $x=5$, $y=5$, $m_A=10^{-9}$, $m_B=10^{-9}$ with starting frequency distributions defined by $a_{me}=b_{me}=c_{me}=0$, $a_{var}=b_{var}=c_{var}=0.5$. Note that these distributions are truncated at zero, which means they generate positive initial values of cooperation and choice. Positive starting values were used because without some initial level of cooperation and choice, mutualism does not evolve (§3, Foster & Wenseleers in press).

the first few generations. However, beyond this it was typically zero, which suggests that it did not play a role in the long-term stability (or instability) of cooperation (data not shown). The initial proportions of individuals with each level of the variables (a , b , c) were taken from normal distributions with means a_{me} , b_{me} , c_{me} and variances a_{var} , b_{var} , c_{var} that were truncated at the minimum and maximum of each variable. A typical simulation ran for 2000 generations (figure 2).

(e) Introducing genetic variability

Choice tends to remove genetic variability. However, in natural populations, some variability will be re-introduced each generation through immigration and mutation. To investigate the effect of reintroduced variability, we used a simple immigration model where a proportion m_A (species A) and m_B (species B) of the population each generation come from a hypothesized source population that is identical to the starting values of the simulation. In addition, we considered the effect of biased mutation, which, when it occurs in males, strongly affects the stability of female choice in models of sexual selection (Pomiankowski *et al.* 1991). By analogy, we investigated the effect of biased mutation towards cheating in species B on the simulation outcome. We assumed that a proportion s of individuals at each level of cooperation mutate and takes on the next level of cooperation down in the matrix, e.g. for $s=0.1$, if all individuals are cooperating fully

($b=1$) then after mutation, 90% will remain at $b=1$ and 10% will have $b=0.9$.

3. RESULTS

(a) Initial evolution of choice and cooperation

The conditions for the initial evolution of cooperation and choice in the model were consistent with previous analyses so we only briefly review them here. Cooperation in each species was only selected with sufficient cooperation in the other (Doebeli & Knowlton 1998; Foster & Wenseleers in press). Furthermore, cooperation in species B was only selected with partner choice in species A (West *et al.* 2002b; Foster & Wenseleers in press). This makes intuitive sense because relatedness is zero among the species B symbionts at the scale of the host, which selects against cooperation in the absence of choice. Selection for partner choice in species A, therefore, critically determined whether mutualism evolved in the model. As shown in West *et al.* (2002a), partner choice was favoured when: (i) the harmful effects of choice on the symbionts f and on the host g were sufficiently low and (ii) the initial variance in species B cooperation (b_{var}) was sufficiently high.

(b) Stability of choice and cooperation

Having established that the conditions for the initial evolution of mutualism were consistent with previous work, we focused upon its subsequent evolution. Importantly, we found that the initial invasion of cooperation

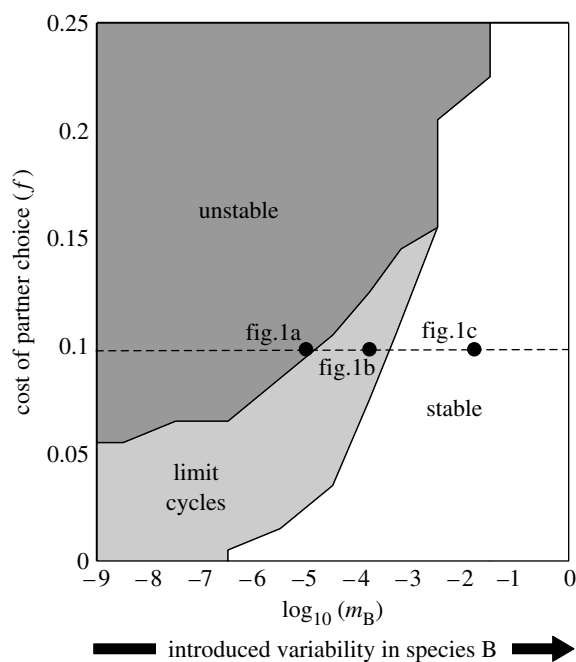


Figure 3. The effect of the cost of partner choice (f) and the level of introduced variability in species B each generation (m_B) on the stability of mutualism (see figure 2). All other parameters are as for figure 2. Note that relatively low levels of migration are required each generation to stabilize mutualism (for the colour version of this figure see the electronic supplementary material).

does not guarantee its maintenance (figure 2a). When choice is sufficiently costly (positive f and/or g), cooperation vanishes eventually even though it is selected for at first. Intuitively, this is because the effect of partner choice is to remove the variability in species B. With no variability, choice is no longer beneficial and becomes costly, which leads to the loss of choice and the collapse of cooperation, first in species B and then species A (figure 2a).

We investigated the effect of introducing variability in species B each generation. This revealed that introduced variability can stabilize choice and, consequently, mutualism (figure 2b–d). Figure 3 shows the simulation outcome for a range of values of f (harm to symbionts from choice, figure 1) and m_B (immigration of species B each generation from source population). When introduced variability is sufficiently high, mutualism is stable even when choice is costly. Our simple mutational model (above) had the same effect and can also maintain partner choice that would otherwise be unstable (figure 2d). Introducing variability in species A (m_A) does not stabilize mutualism equally easily. Exploration of the model revealed that only by introducing species A individuals that have a high level of choice (c) each generation could mutualism be stabilized, but we lack a biologically feasible explanation for such an influx of choosy hosts. We therefore focus here upon the effects of variability in species B (figures 2 and 3), which seems more biologically likely.

4. DISCUSSION

Our model shows that although partner choice and cooperation may often initially be selected in mutualisms (West *et al.* 2002a,b; Sachs *et al.* 2004; Foster & Wenseleers *in press*), they will not always persist.

Specifically, partner choice by the host reduces variability in the symbiont, which in turn reduces the benefit of choice. At the extreme that symbionts cooperate perfectly, choice no longer has any benefit to the host at all. This leads to the loss of partner choice when it is costly (figures 2 and 3). Is partner choice sufficiently costly in natural systems for this effect to occur? Assessing the cost of partner choice represents an empirical challenge for the future (West *et al.* 2002a). However, the magnitudes of costs when choice is lost in our model are not extreme and correspond to a few percent reductions in host fitness. In figure 2a, for example, the mean fitness cost of choice to hosts from both the direct effect on the host (g) and the indirect effect through the symbionts (f) does not rise above 5% and, at the critical point where cooperation in species B disappears, is less than 2%. This suggests partner choice systems associated with even low costs can be difficult to maintain (figures 2 and 3).

Partner choice in mutualisms, therefore, raises a familiar conundrum for evolutionary theory: what maintains genetic variability in a given population in the face of selection (e.g. Barton & Keightley 2002)? In our case, we find that a small influx of immigrants or mutants with a tendency to cooperate less (i.e. cheaters) generates sufficient genetic variability to stabilize choice. This raises an important parallel with models of sexually selected female choice (Kokko *et al.* *in press*). In mate choice for indirect benefits such as genes for highly viable offspring, it is challenging to explain why unanimous female choice does not erode the genetic variation that is the reason to distinguish between different males as sires. Yet without a reason for females to be choosy, males should not maintain costly ornamentation (Kirkpatrick & Ryan 1991; Tomkins *et al.* 2004). Analogous to our findings, it has been shown that female choice is stabilized by a negative mutational bias on a sexually selected male trait (Pomiankowski *et al.* 1991) or condition that is then signalled by the male trait (Iwasa *et al.* 1991).

Does this analogy mean that partner choice is equally difficult to explain as female preferences for elaborate male traits—where after decades of study the maintenance of preferences for indirect benefits are still being hotly debated (e.g. Kokko *et al.* 2003; Qvarnström *et al.* 2006)? Our model does not give a direct answer to this question, but we suspect not. Unlike many cases of female choice, it is clear that partner choice provides direct benefits e.g. nutrients rather than genes. This means that environmental variation can also promote the evolution of choice in mutualisms and boost any sources of genetic variability, an effect that will not occur with female choice in the absence of direct benefits.

Assessing variation in the degree of cooperation by mutualists, and whether it is environmentally or genetically based, is an interesting challenge for empirical work. That said, there are already some studies that offer broad support for our prediction that standing variation can be a requirement for the evolution of mutualism, including yuccas where some plants sustain yucca moth larvae in their fruits, but others do not (Bao & Addicott 1998), some nectarless plants in populations of honey mesquite (Golubov *et al.* 1999), strains of the symbiotic algae of the upside-down jellyfish that invest little in their host (Sachs & Wilcox 2006) and non-fixing strains of rhizobial bacteria in legumes (Thrall *et al.* 2000). The last example is particularly relevant because legumes have also been

shown to engage in partner choice by sanctioning less cooperative rhizobia (Kiers *et al.* 2003; Simms *et al.* 2006). In addition, many mutualisms have third-party cheater species that exploit the mutualists (Ferriere *et al.* 2002; Bronstein 2003; Wilson *et al.* 2003), such as in the fungus-growing ants and their garden fungi. Ants invest energy and time selecting and feeding their own fungi over foreign strains, and poor tending of the fungus garden leaves them prone to destruction by a specialist parasite species (Currie & Stuart 2001; Mueller *et al.* 2004; Poulsen & Boomsma 2005). The presence of the cheater species, therefore, maintains the incentive for partner choice by the workers.

It is intriguing to consider that such processes may be important for cooperation in general. Enforcement mechanisms that are analogous to partner choice are important in the evolution of within-species cooperation, including the policing and punishment of rebellious individuals and cheaters (Frank 2003; Gardner & West 2004; Sachs *et al.* 2004; Ratnieks *et al.* 2006). Like partner choice, these mechanisms will tend to reduce the variation in cooperativity among individuals and so the incentive for their own maintenance.

The evolution of cooperation may often rest upon something of a paradox. Mechanisms of enforcement can be required to maintain cooperation but, when costly, these mechanisms will only be maintained when there is some way for cheaters to persist. In this case, it is the cheating that ultimately stabilizes the evolution of cooperation.

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