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Cheating and the evolutionary stability of mutualisms

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Interspecific mutualisms have been playing a central role in the functioning of all ecosystems since the early history of life. Yet the theory of coevolution of mutualists is virtually nonexistent, by contrast with well-developed coevolutionary theories of competition, predator–prey and host–parasite interactions. This has prevented resolution of a basic puzzle posed by mutualisms: their persistence in spite of apparent evolutionary instability. The selective advantage of 'cheating', that is, reaping mutualistic benefits while providing fewer commodities to the partner species, is commonly believed to erode a mutualistic interaction, leading to its dissolution or reciprocal extinction. However, recent empirical findings indicate that stable associations of mutualists and cheaters have existed over long evolutionary periods. Here, we show that asymmetrical competition within species for the commodities offered by mutualistic partners provides a simple and testable ecological mechanism that can account for the long-term persistence of mutualisms. Cheating, in effect, establishes a background against which better mutualists can display any competitive superiority. This can lead to the coexistence and divergence of mutualist and cheater phenotypes, as well as to the coexistence of ecologically similar, but unrelated mutualists and cheaters.

Keywords: mutualism; evolutionary stability; cheating; asymmetrical competition; evolutionary branching

1. INTRODUCTION

Mutually beneficial interactions between members of different species play a central role in all ecosystems (Boucher *et al.* 1982; Thompson 1994; Bronstein 2001*a*). Despite the widespread occurrence and obvious importance of mutualistic interactions, the theory of mutualistic coevolution is virtually nonexistent (but see Kiester *et al.* 1984; Law 1985; Frank 1994, 1996; Law & Dieckmann 1998), by contrast with the well-developed coevolutionary theory of competition, host–parasite and predator–prey interactions (surveyed in Roughgarden (1983); Frank (1996), Abrams (2000), respectively). This lack of theory prevents resolution of the most basic and longstanding puzzle posed by mutualisms: their persistence in spite of apparent evolutionary instability. Interspecific mutualisms inherently exhibit conflicts of interest between the interacting species in that selection should favour cheating strategies, which are displayed by individuals that reap mutualistic benefits while providing fewer commodities to the partner species (Axelrod & Hamilton 1981; Soberon Mainero & Martinez del Rio 1985; Bull & Rice 1991; Addicott 1996). Slight cheats arising by mutation could gradually erode the mutualistic interaction, leading to dissolution or reciprocal extinction (Roberts & Sherratt 1998; Doebeli & Knowlton 1998). Although cheating has been assumed to be under strict control, recent empirical findings indicate that cheating is rampant in most mutualisms (Poulin & Grutter 1996; Johnson *et al.* 1997; Foster & Delay 1998; Irwin & Brody 1998; Addicott & Bao 1999; Currie *et al.* 1999); in some cases, cheaters have been associated with mutualisms over long spans of evolutionary time (Pellmyr *et al.* 1996; Machado *et al.* 1996; Addicott 1985). Here, we offer a general explanation for the evolutionary origin of cheaters and the unexpected stability of mutualistic associations subject to cheating.

2. MODEL CONSTRUCTION AND MATHEMATICAL ANALYSIS

The following model concerns a two-species, obligate mutualism. Each species has a continuous phenotypic trait that measures the rate at which commodities (i.e. a reward like nectar or a service like pollination) are provided to the partner. Provision of commodities is assumed to be costly in terms of reproduction or survival, and cheating phenotypes that produce commodities at a lower rate incur a reduced cost (Boucher *et al.* 1982; Maynard Smith & Szathmary 1995; Herre *et al.* 1999; Bronstein 2001*b*). Also, commodities provided by either species represent a limited resource for the partner species: there is intraspecific competition for commodities (Addicott 1985; Iwasa *et al.* 1995; Bultman *et al.* 2000). Our analysis focuses on the evolutionary consequences of this form of competition nested within the mutualistic interaction.

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(a) *Ecological dynamics*

The mutualistic interaction between species X (density x) and species Y (density y) is described by a simple Lotka–Volterra model

$$\frac{dx}{dt} = [-r(u) - cx + vy(1 - \alpha x)]x, \tag{2.1a}$$

$$\frac{dy}{dt} = [-s(v) - dy + ux(1 - \beta y)]y. \tag{2.1b}$$

The mutualistic traits u and v are measured as per capita rates of commodities trading; thus, ux and vy represent the probabilities per unit time that a partner individual receives benefit from a mutualistic interaction. Intraspecific competition for commodities provided by the partner species is expressed by the linear density-dependent factors $(1 - \alpha x)$ and $(1 - \beta y)$ (Wolin 1985). The terms $-cx$ and $-dy$ measure the detrimental effect of intraspecific competition for other resources. The mutualism being obligate, the intrinsic rates of increase, $-r(u)$ and $-s(v)$, are negative, and $r(u)$ and $s(v)$ increase with u and v respectively, to reflect the direct cost of producing commodities. A standard analysis of the ecological model shows that the extinction state $x = 0$, $y = 0$ is always a locally stable equilibrium. Depending on the trait values u and v, there may also exist two positive equilibria, one being stable (node) and the other being unstable (saddle). These equilibria, whenever they exist, are solutions of

$$-r(u) - cx + vy[1 - \alpha x] = 0 \tag{2.2a}$$

$$-s(v) - dy + ux[1 - \beta y] = 0, \tag{2.2b}$$

and in the case where they do exist, we denote the stable one by $(\hat{x}, \hat{y})$. The transition between the two cases (zero or two equilibria apart from the extinction state) is caused by a saddle-node bifurcation. The corresponding bifurcation curve is the closed, ovoid curve depicted in figure 1*a–c*, which separates a region of trait values that lead to extinction from a domain, D, of traits that correspond to viable ecological equilibria. How this ovoid curve is calculated is explained in Appendix A.

(b) *A mathematical approximation of mutation-selection processes*

To construct a mathematical model for the joint evolution of the partners' rates of commodity provision, we assume that individuals' births, interactions and deaths occur on a short, ecological time-scale over which the species' abundances quickly equilibrate. Rare mutations in the phenotypes arise on a long, evolutionary time-scale. The evolutionary process comprises a sequence of trait substitutions caused by selection of successful mutants that spread to fixation on the ecological time-scale. Thus, the evolutionary dynamics of the rates of commodity provision follow the fitness gradients generated by the underlying ecological dynamics (Hofbauer & Sigmund 1990; Abrams *et al.* 1993). By assuming the time-scale separation of ecological and evolutionary processes, the rates of change of traits u and v are given by

$$\frac{du}{d\tau} = k_u (\ldots)\, \hat{x}(\partial W_X/\partial u_{mut})_{u_{mut} = u} \tag{2.3a}$$

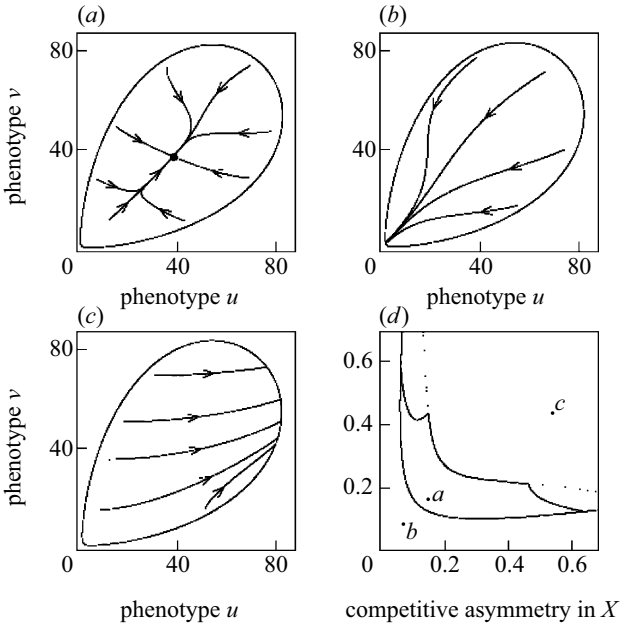

Figure 1. Competitive asymmetry and the evolutionary persistence of mutualism. The ovoid domain (computed from equation (A 4)) delineates the phenotypic trait values u and v that make the mutualistic association ecologically viable. Each orientated curve (computed from equation (2.3)) depicts an evolutionary trajectory starting from a different ancestral phenotypic state. (*a*) Convergence towards an evolutionary singularity that is ecologically viable (black circle). Specific degrees of competition asymmetry are $\alpha' = 0.035$ and $\beta' = 0.035$. (*b*) Evolutionary suicide through selection of ever-reduced mutualistic investments ($\alpha' = 0.01$ and $\beta' = 0.01$). (*c*) Evolutionary suicide by runaway selection for ever-increased mutualistic investments ($\alpha' = 0.30$ and $\beta' = 0.20$). (*d*) Dependence of the evolutionary dynamics regime on the degrees of competitive asymmetry in species X and Y, as measured respectively by $\sqrt{\alpha'}$ (horizontal axis) and $\sqrt{\beta'}$ (vertical axis). Hatched region, convergence to an evolutionary singularity that is ecologically viable; white area, evolutionary suicide. Points *a*, *b*, *c* correspond to previous panels. Numerical analysis performed with $r(u) = 0.001(u + u^2)$, $s(v) = 0.001(v + v^2)$, $c = 1$, $d = 2$. To investigate the existence and stability of evolutionary singularities, we performed extensive numerical bifurcation analyses with respect to the degrees of asymmetry α' and β'; these parameters have the nice property of not influencing the ovoid domain D of traits (u, v) that ensure ecological persistence (figure 1*a–c*). In general, there is a wing-shaped region of parameters α' and β' in which the evolutionary singularity, denoted hereafter by (u^*, v^*), exists as a stable, hence attracting, equilibrium node within D (figure 1*d*). This region is bounded by bifurcation curves of the adaptive dynamical system that correspond to different routes along which the attracting evolutionary singularity can be lost: by collision with an unstable saddle, by collision with the boundary of D, or through supercritical Hopf and homoclinic bifurcations.

$$\frac{dv}{d\tau} = k_v (\ldots)\, \hat{y}(\partial W_Y/\partial v_{mut})_{v_{mut} = v} \tag{2.3b}$$

(Dieckmann & Law 1996). Parameters k_u and k_v denote evolutionary rates that depend on the mutation rate and mutation step variance; $\hat{x}$ and $\hat{y}$ are the equilibrium population densities of resident phenotypes u and v (the likelihood of a mutation is proportional to the number of

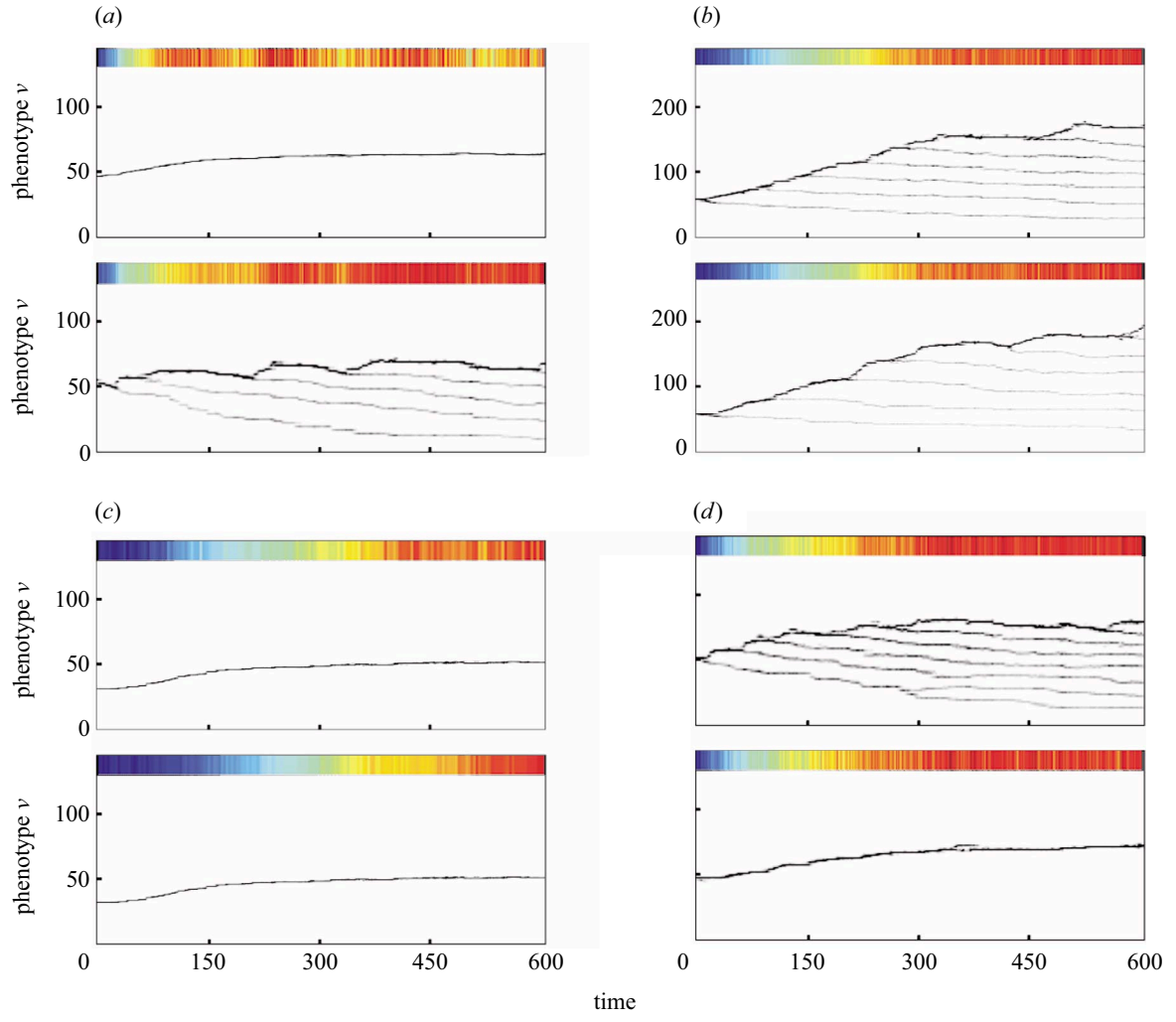

Figure 2. Evolutionary branching and the diversification of mutualisms. Evolutionary trajectories show the distribution of phenotypes (in scales of grey: black, highest frequency; white, absence) across time. All trajectories start near the same attracting evolutionary singularity, $u^* = 50$, $v^* = 50$. After convergence to this point, selection may turn disruptive and evolutionary branching may occur in either species or both depending on whether u^* and v^* are above branching thresholds u_b and v_b (cf. § 2*d*). Left-hand column, $u^* < u_b$; right-hand column, $u^* > u_b$; bottom row, $v^* < v_b$; top row, $v^* > v_b$. (*a*, *d*) Unilateral diversification. (*b*) Bilateral diversification. (*c*) No diversification. Colour bars indicate the amount of commodities provided on average to each individual of the partner species (scaled between 0 = minimum, in blue, and 1 = maximum, in red). Asymmetrical competition functions and details on simulation schemes are given in Appendices A and B. (*a*) $\alpha(0) = 2.08$, $\alpha' = 0.04$, $\alpha'' = 0$, $\beta(0) = 2.05$, $\beta' = 0.4$, $\beta'' = -9.16$; (*b*) $\alpha(0) = 1.1$, $\alpha' = 0.4$, $\alpha'' = -7.2$, $\beta(0) = 2.05$, $\beta' = 0.4$, $\beta'' = -9.16$; (*c*) $\alpha(0) = 2.08$, $\alpha' = 0.04$, $\alpha'' = 0$, $\beta(0) = 4.0$, $\beta' = 0.02$, $\beta'' = 0$; (*d*) $\alpha(0) = 1.1$, $\alpha' = 0.4$, $\alpha'' = -7.2$, $\beta(0) = 4.0$, $\beta' = 0.02$, $\beta'' = 0$. Other parameter values are as in figure 1.

reproducing individuals); $W_X := W_X(u_{mut}, u, v)$ and $W_Y := W_Y(v_{mut},u,v)$ are the invasion fitnesses, defined as rates of increase from initial rarity (Metz *et al.* 1992; Ferriere & Gatto 1995) of a mutant phenotype u_{mut} of species X and of a mutant phenotype v_{mut} of species Y in a resident association u, v; W_X and W_Y are given by

$$W_X(u_{mut},u,v) = -r(u_{mut}) - c\hat{x} + v[1 - \alpha(u_{mut} - u)\hat{x}]\hat{y}, \tag{2.4a}$$

$$W_Y(v_{mut}, u, v) = -s(v_{mut}) - d\hat{y} + u[1 - \beta(v_{mut} - v)\hat{y}]\hat{x}. \tag{2.4b}$$

(c) *Evolutionary dynamics under symmetrical versus asymmetrical competition*

With symmetrical competition, the competition coefficients $\alpha(u_{mut} - u)$ and $\beta(v_{mut} - v)$ are actually independent of $u_{mut} - u$ and $v_{mut} - v$, respectively; therefore we have

$$\left(\frac{\partial W_X}{\partial u_{mut}}\right)_{u_{mut} = u} = -r'(u), \tag{2.5a}$$

$$\left(\frac{\partial W_Y}{\partial v_{mut}}\right)_{v_{mut} = v} = -s'(v). \tag{2.5b}$$

Since r and s are increasing functions of their arguments, from any ancestral state the process of mutation-selection causes the monotonic decrease of the traits u and v towards 0. All evolutionary trajectories eventually hit the boundary of ecological viability; in other words, evolution leads to extinction of the system.

Asymmetrical competition between two phenotypes X_1 and X_2 providing commodities at rates u_1 and u_2,

respectively, is modelled by replacing the constant competition coefficient α with a sigmoid function of the difference in the rate of commodity provision $u_1 - u_2$ (Matsuda & Abrams 1994; Law *et al.* 1997; Kisdi 1999); an example of such a sigmoid function that we used to perform our numerical simulations is given in Appendix B. A large, positive difference in the rate of commodity provision implies that α approaches its minimum value, whereas a large, negative difference results in a value of α close to its maximum. The absolute value of the slope of the tangent to this curve at zero provides a measure of the degree of competitive asymmetry. The first-order effect on fitness induced by a small difference in the rate of commodity provision is then measured by the derivative

$$\left(\frac{\partial W_X}{\partial u_{\mathrm{mut}}}\right)_{u_{\mathrm{mut}}=u} = -r'(u) + \alpha' v \hat{x} \hat{y}, \tag{2.6a}$$

where $\alpha' \equiv |\alpha'(0)|$ is the degree of competitive asymmetry. Likewise, by introducing the asymmetrical competition function β for species Y, we get

$$\left(\frac{\partial W_Y}{\partial v_{\mathrm{mut}}}\right)_{v_{\mathrm{mut}}=v} = -s'(v) + \beta' u \hat{x} \hat{y}, \tag{2.6b}$$

with $\beta' \equiv |\beta'(0)|$. The intersection point of the isoclines $(\partial W_X/\partial u_{\mathrm{mut}})_{u_{\mathrm{mut}}=u} = 0$ and $(\partial W_Y/\partial v_{\mathrm{mut}})_{v_{\mathrm{mut}}=v} = 0$ defines a so-called evolutionary singularity (Geritz *et al.* 1997) that may either attract or repel phenotype trajectories (locally).

(d) *Conditions for a mutualist and a slight cheater to invade each other*

At the attracting evolutionary singularity (AES), the first-order effect on fitness of a slight change in the rate of commodity provision vanishes and further evolutionary dynamics depend on the second-order derivatives

$$\left(\frac{\partial^2 W_X}{\partial u_{\mathrm{mut}}^2}\right)_{u_{\mathrm{mut}}=u} = \frac{-r''(u^*) + \alpha'' v^* x^* y^*}{2}, \tag{2.7a}$$

$$\left(\frac{\partial^2 W_Y}{\partial v_{\mathrm{mut}}^2}\right)_{v_{\mathrm{mut}}=v} = \frac{-s''(v^*) + \beta'' u^* x^* y^*}{2}, \tag{2.7b}$$

where $x^* = \hat{x}(u^*, v^*)$, $y^* = \hat{y}(u^*, v^*)$ and $\alpha'' = -\alpha''(0)$, $\beta'' = -\beta''(0)$. If the second-order derivative given by equation (2.7*a*) (equation (2.7*b*), respectively) is negative, the AES is a fitness maximum for species X (for species Y), that is, the evolution of trait u (v) comes to a halt at u^* (v^*). If the second-order derivative is positive, species X (Y) encounters a fitness minimum at u^* (v^*) (Abrams *et al.* 1993), with reciprocal invasibility of mutants surrounding u^* (v^*) as a consequence. Reciprocal invasibility around an AES is an important property that indicates that selection turns disruptive and evolutionary branching takes place (Geritz *et al.* 1997). The conditions for reciprocal invasibility around u^* and v^*, respectively, read

$$\frac{\alpha''}{\alpha'} > \frac{r''(u^*)}{r'(u^*)}, \tag{2.8a}$$

$$\frac{\beta''}{\beta'} > \frac{s''(v^*)}{s'(v^*)}. \tag{2.8b}$$

For example, specifying r and s as $r(u) = r_0 + r_1 u + (r_2/2)u^2$ and $s(v) = s_0 + s_1 v + (s_2/2)v^2$, reciprocal invasibility occurs at the AES in species X or Y if u^* or v^* exceed thresholds given by $u_{\mathrm{b}} = (\alpha'/\alpha'') - (r_1/r_2)$ and $v_{\mathrm{b}} = (\beta'/\beta'') - (s_1/s_2)$, where the subscripted b stands for 'branching'.

(e) *How does evolutionary divergence affect the total amount of commodities provided to partners?*

Consider two reciprocally invasible phenotypes u_1 and u_2 with equilibrium densities $\hat{x}_1$ and $\hat{x}_2$, around the AES u^* in species X, such that $u_1 = u^* + \partial u$ and $u_2 = u^* - \partial u$. The total mutualistic commodities offered to any Y individual is

$$\begin{aligned} U &= (u^* + \partial u)\hat{x}_1 + (u^* - \partial u)\hat{x}_2 \\ &= u^*(\hat{x}_1 + \hat{x}_2) + \partial u(\hat{x}_1 - \hat{x}_2). \end{aligned} \tag{2.9a}$$

At u^*, this amount is

$$U^* = u^* \frac{-r(u^*) + v^* y^*}{c + \alpha(0) v^* y^*}. \tag{2.9b}$$

Up to second-order terms, a Taylor expansion of U for small ∂u reads

$$U = u^* \frac{-r(u^*) + v^* y^*}{c + (\alpha(0) - (\alpha'^2/\alpha''))v^* y^*}. \tag{2.9c}$$

Therefore, whenever the competition asymmetry is such that $\alpha'' > 0$, the total amount of commodities always increases locally through an AES where evolutionary branching occurs. The same reasoning holds for species Y.

3. BIOLOGICAL IMPLICATIONS

In this model, the mutualistic pair is ecologically stable as long as the rates of commodity provision are neither extremely low nor too high. At the boundary of the domain D of the trait space that permits ecological persistence (i.e. the ovoid curve in figure 1*a–c*), the system undergoes a catastrophic bifurcation and collapses abruptly (cf. § 2*a*). In the short term, mutualistic populations within the persistence region thus reach a stable ecological equilibrium. However, if individuals compete with equal success for the commodity provided by the other species, regardless of how much those individuals invest in mutualism (symmetrical competition), the long-term evolutionary dynamics will always drive the association towards the boundary of the coexistence region D, irrespective to the ancestral state (equation (2.4)). The mutualism erodes because cheating mutants that invest less in mutualism will be under no competitive disadvantage and thus will always be able to invade, ultimately driving the partner species to extinction. Thus, ecological stability alone by no means provides a sufficient condition for the evolutionary persistence of a mutualism subject to natural selection.

Although such 'evolutionary suicide' would be a general property of mutualisms involving symmetrical competition for commodities, as a rule, competition in nature is asymmetrical (Brooks & Dodson 1965; Lawton 1981; Karban 1986; Callaway & Walker 1997). Clearly, if any competitive asymmetry within either species were to give an advantage to individuals that provide fewer commodities,

there would be no way out of the evolutionary suicide described above. However, individuals often discriminate among partners according to the quantity of rewards they provide and associate differentially with higher reward producers (Bull & Rice 1991; Christensen *et al.* 1991; Mitchell 1994; Anstett *et al.* 1998). Our analysis shows that such a competitive premium for providing more commodities leads to a much richer range of evolutionary outcomes.

Competitive asymmetry in effect generates a selective force that can counter the pressure for reducing the provision of commodities (equation (2.6)): at intermediate degrees of competitive asymmetry, the mutualistic association evolves towards a viable evolutionary singularity (figure 1*a*,*d*). If the asymmetry is too weak in either species, selective pressure favouring lower provision of commodities will predominate in that population. As the total amount of commodities offered to the partner species decreases, the selective pressure induced by competitive asymmetry in the partner is weakened and selection for reduced provision of commodities takes over on that side of the interaction, too; extinction is the inexorable outcome (figure 1*b*). If the asymmetry is too strong on either side, the selective pressure favouring the provision of more commodities will predominate, causing runaway selection until the costs incurred are so large that the association becomes nonviable and extinction is again the outcome (figure 1*c*).

Assuming that the degrees of competitive asymmetry are within the range that allows evolution to an ecologically viable evolutionary singularity, two things can happen at this point: either selection stabilizes the association at the evolutionary singularity, or selection turns disruptive (figure 2). In the latter case, all neighbouring phenotypes are reciprocally invasible, and evolutionary branching (Geritz *et al.* 1997) results. That is, a strain of better mutualists and a strain of cheaters coexist and start diverging. Whether selection is stabilizing or disruptive at the evolutionary singularity is chiefly determined by (cf. equation (2.8)):

(i) the nature of the asymmetry; and
(ii) the cost to the individual of providing commodities.

We say that the asymmetry is 'rewarding' if its main effect is to confer a strong competitive advantage to individuals that provide more commodities; with our notations from § 2, this occurs in species X when $\alpha'' < 0$ and in species Y when $\beta'' < 0$. By contrast, 'punishing' asymmetry (occurring when $\alpha'' > 0$ in species X and $\beta'' > 0$ in species Y) primarily induces a strong competitive disadvantage to individuals that provide fewer commodities. We say that the costs are 'accelerating' (respectively, 'decelerating') if a large increase in the rate of producing commodities impacts the cost disproportionately more (disproportionately less) than a small increase. The mathematical translation of cost acceleration (respectively, deceleration) writes $r'' > 0$ ($r'' < 0$) in species X and $s'' > 0$ ($s'' < 0$) in species Y. Both rewarding and punishing asymmetry, and accelerating and decelerating costs, appear to exist in mutualisms (Iwasa *et al.* 1995; Bultman *et al.* 2000).

Disruptive selection occurs at the evolutionary singularity of a species incurring a decelerating cost of mutualism if the asymmetry is rewarding or even slightly punishing (equation (2.8)). In this case, the competitive advantage to a slightly better mutualist is sufficient to overcome the increase in costs it experiences. At the same time, a slightly less mutualistic type can invade a population of better mutualists as long as the competitive disadvantage it suffers is not too large, because of the benefit from reduced costs (this sets a limit on how punishing the asymmetry may be). Likewise, equation (2.8) shows that a species characterized by an accelerating cost of mutualism undergoes disruptive selection at the evolutionary singularity only if competitive asymmetry is rewarding. In this case, a slightly less mutualistic type does not gain much through cost reduction and can invade a population of better mutualists only if its competitive disadvantage is small; a slightly better mutualist incurs a relatively large cost and needs a sufficient competitive advantage to invade successfully a population of cheaters.

Disruptive selection at an evolutionary singularity opens an evolutionary route to the coexistence of phenotypes ranging from good mutualists that provide large amounts of commodities, to cheaters that are almost purely exploitative (figure 2). Remarkably, the repeated evolution of cheating phenotypes triggered by rewarding competitive asymmetry is accompanied by a tendency for the total amount of commodities offered to partners to increase (colour bars in figure 2; mathematical underpinning in § 2*e*). The reduced provision of commodities by evolving cheaters is more than compensated for by the concomitant evolution of better mutualists. Far from always driving mutualism to extinction, the evolution of cheating within one party actually coincides with an increase in the benefits to the other party.

4. CONCLUSION

Our phenotypic model assumes asexual reproduction and would be most appropriate for the evolution of prokaryotic, symbiotic organisms. Sexual reproduction is likely to affect evolutionary branching, because mating between individuals would generate intermediate types, preventing distinct phenotypic branches from evolving. Yet the outcome might eventually be sympatric speciation, because intermediate phenotypes would have lower fitness than the extremes, giving the conditions under which genes for assortative mating would spread (Dieckmann & Doebeli 1999; Kisdi & Geritz 1999). Another possible outcome would be for a sexual mutualistic species near a branching state to be invaded by another species with similar ecological properties but with a lower or higher rate of commodity provision. Phenotypic evolution in effect leads to ecological conditions that would permit two species providing slightly different amounts of commodities to coexist and to start diverging into a better mutualist and a cheater. This prediction matches the phylogenetic pattern documented for the well-studied yucca–yucca moth mutualism, in which mutualists and cheaters are ecologically similar in many respects but are not sister species (Pellmyr & Leebens-Mack 1999).

Mutualist and cheater phenotypes or species are known empirically to coexist in many mutualisms (Machado *et al.* 1996; Pellmyr & Leebens-Mack 1999; Després &

Jaeger 1999; Bronstein 2001*b*). Our theory shows that asymmetrical competition for commodities can explain the long-term persistence of mutualistic partnerships in spite of the evolution or incorporation of cheaters. Competition for benefits from partners is a cornerstone in the theory of sexual selection, but surprisingly, its effects had been minimally evaluated in the context of the evolution of cooperative behaviour (Noë *et al.* 1991; Noë & Hammerstein 1995). Cheaters in effect provide a background against which better mutualists can display any competitive superiority. The approach we have used is based on the simplest possible ecological model (similar to the model of Frank (1994) for the origin of symbiosis); we have analysed other simple ecological models of mutualism, as well as more detailed models of particular biological systems, with similar results (Gauduchon *et al.* 2002; Law *et al.* 2001). We predict that different evolutionary trajectories should be found in mutualisms characterized by different functional forms of competitive asymmetry and investment costs. Documenting the shapes of these functions is therefore an important avenue for future empirical research.

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APPENDIX A: ECOLOGICAL DYNAMICS

The ecological system equation (2.1) possesses either zero or two equilibria in the positive orthant. Equilibria are sought by solving the system $\mathrm{d}x/\mathrm{d}t = 0$, $\mathrm{d}y/\mathrm{d}t = 0$, which yields

$$y = \frac{1\,r + cx}{v1 - \alpha x}, \tag{A 1a}$$

$$x = \frac{1\,s + dy}{u1 - \beta y}. \tag{A 1b}$$

Since $\mathrm{d}y/\mathrm{d}x > 0$ and $\mathrm{d}x/\mathrm{d}y > 0$, it follows that the three potential equilibria (the origin and the two positive equilibria) are ordered in the phase portrait, thus defining a 'small' equilibrium and a 'large' equilibrium.

The condition separating the two cases (zero or two positive equilibria) is a saddle-node bifurcation. To determine the condition that must be satisfied by the model parameters for this bifurcation to occur, we first recast equation (A 1*a*) into the single equation

$$Ay^2 + By + C = 0, \tag{A 2}$$

where

$$A = uv\beta + v\alpha d, \tag{A 3a}$$

$$B = -uv - ur\beta + v\alpha s + cd, \tag{A 3b}$$

$$C = ur + cs. \tag{A 3c}$$

Notice that A and C have the same sign (+), therefore the two roots of equation (A 2), should they exist, are both positive or both negative. The bifurcation condition obtains from taking the discriminant $B^2 - 4AC$ of equation (A 2) as equal to zero, which leads to the following quartic relationship between the mutualistic traits u and v:

$$\begin{aligned} &u^2v^2 - 2\beta ru^2v - 2\alpha suv^2 + \beta^2r^2u^2 \\ &\quad - 2(cd + \alpha\beta rs + 2c\beta s + 2d\alpha r)uv + \alpha^2s^2v^2 \\ &\quad - 2cd\beta ru - 2cd\alpha sv + c^2d^2 = 0. \end{aligned} \tag{A 4}$$

Equation (A 4) defines a curve in the (u, v) trait space (the ovoid curve depicted in figure 1*a–c*) that bounds the domain D of ecological viability of the mutualistic association. The fact that the large equilibrium is actually stable, and that the small one is a saddle, can be verified by looking at the Jacobian $\boldsymbol{J}$ of equation (2.1) evaluated at the equilibrium

$$\boldsymbol{J} = \begin{bmatrix} -(c + v\alpha y)x & v(1 - \alpha x)x \\ u(1 - \beta y)y & -(d + u\beta x)y \end{bmatrix}. \tag{A 5}$$

One may easily check that the trace of $\boldsymbol{J}$ is negative; the determinant of $\boldsymbol{J}$ is given by

$$\det \boldsymbol{J} = xy[(cd + uc\beta x + vd\alpha y + uv\alpha x + uv\beta y) - uv]. \tag{A 6}$$

Notice that the term between parentheses is always positive. At the bifurcation, one has $\det \boldsymbol{J} = 0$ and there is a single equilibrium, but the two equilibria that appear for a small parameter perturbation are one smaller, and the other larger than the bifurcation equilibrium. Since the negative term in the bracketed part of equation (A 6) does not depend upon x and y, while the positive term increases with x and y, it follows that the large equilibrium is characterized by $\det \boldsymbol{J} > 0$ and is therefore stable; by contrast, the small equilibrium is characterized by $\det \boldsymbol{J} < 0$ and is, therefore, a saddle.

APPENDIX B: STOCHASTIC, INDIVIDUAL-BASED SIMULATIONS OF EVOLUTIONARY DYNAMICS

Our mathematical analysis (§ 2) is based on the time-scale separation of ecological and evolutionary processes. This assumption has been relaxed in the numerical simulations of the mutation-selection process underlying figure 2, by making use of a stochastic, individual-based model in which individuals of species X with phenotype u die at rates $r(u) + cN_X/K$, where N_X is X's population size and K is the carrying capacity (1000 for both species) and give birth at rates $(\Sigma_k \nu_k)\cdot(1 - \Sigma_i \alpha(u - u_i)/K)$, where the sums Σ are respectively taken over all Y individuals (indexed by subscript k) and all X individuals (indexed by subscript i). Similar expressions apply to the death and birth rates of species Y individuals. In both species, offspring usually inherit their parent's phenotype, but mutations occur at small rates (set to 0.001); the phenotypic value of a mutant is normally distributed around the parent's trait (variance = 1.0). Asymmetrical competition functions are

$$\alpha(u_2 - u_1) = 2\kappa_X\{1 - (1 + \gamma_X e^{-\omega_X(u_2 - u_1)})^{-1}\} \tag{B 1}$$

and

$$\beta(\nu_2 - \nu_1) = 2\kappa_Y\{1 - (1 + \gamma_Y e^{-\omega_Y(\nu_2 - \nu_1)})^{-1}\}. \tag{B 2}$$

To run the simulations presented in figure 2, the parameters κ_X, γ_X and ω_X (κ_Y, γ_Y and ω_Y, respectively) were adjusted to yield the prescribed values of $\alpha(0)$, α' and α'' ($\beta(0)$, β' and β'' respectively).

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