doi:10.1111/j.1420-9101.2008.01505.x

Mutualism, market effects and partner control

R. A. JOHNSTONE* & R. BSHARY†

*Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK
†Institute of Biology, University of Neuchatel, Neuchatel, Switzerland

Keywords:

biological markets;
cleaner fish;
cooperation;
mutualism;
partner control;
punishment;
reciprocal altruism.

Abstract

Intraspecific cooperation and interspecific mutualism often feature a marked asymmetry in the scope for exploitation. Cooperation may nevertheless persist despite one-sided opportunities for cheating, provided that the partner vulnerable to exploitation has sufficient control over the duration of interaction. The effectiveness of the threat of terminating an encounter, however, depends upon the ease with which both the potential victim and the potential exploiter can find replacement partners. Here, we extend a simple, game-theoretical model of this form of partner control to incorporate variation in the relative abundance of potential victims and exploiters, which leads to variation in the time required for individuals of each type to find a new partner. We show that such market effects have a dramatic influence on the stable level of exploitation (and consequent duration of interaction). As the relative abundance of victims decreases, they become less tolerant to exploitation, terminating encounters earlier (for a given level of exploitation), whereas exploiters behave in a more cooperative manner. As a result, the stable duration of interaction actually increases, despite the decreasing tolerance of the victims. Below a critical level of relative victim abundance, the model suggests that the cost of finding a replacement partner becomes so great that it does not pay to exploit at all.

Introduction

Many instances of cooperation in nature feature a marked discrepancy between partners in the scope for exploitation (Bshary & Bronstein, 2004). For instance, when a client fish visits the territory of a cleaner wrasse (*Labroides dimidiatus*), it stands to gain by removal of ectoparasites and dead or infected tissue (reviews: Losey *et al.* 1999, Côté, 2000). At the same time, it runs the risk of exploitation by a 'cheating' cleaner that bites live tissue in addition to parasites (Grutter & Bshary, 2003). Although predatory clients may be able to retaliate (or even pre-empt) such exploitation by consuming the cleaner (Trivers 1971, Bshary, 2001), the great majority of client species are nonpredatory, feeding on algae and plankton, and cannot exploit cleaners as prey (Bshary, 2001). What then prevents a cleaner from biting such a client?

Even in cases where the opportunity for direct exploitation is one sided, a potential victim may be able to escape from its exploiter and so terminate their interaction. This 'exit threat' potentially provides a simple form of partner control, as early termination in response to exploitation may entail a loss of potential mutualistic benefits (and of the opportunity for further exploitation) on the part of the exploiter (Schuessler, 1989; Hauk, 2001; West *et al.*, 2002; Frank, 2003; Sachs *et al.*, 2004; Cant & Johnstone 2006; Foster & Wenseleers, 2006). In the case of the cleaner wrasse, for example, if a client that is bitten leaves in response, this ends the opportunity for further profitable cooperation (or exploitation). According to the classificatory scheme of Sachs *et al.* (2004) and Foster & Wenseleers (2006), such termination behaviour constitutes a simple form of partner choice, and favours cooperation through directed reciprocation.

Johnstone & Bshary (2002) developed a simple, game-theoretical model to demonstrate the plausibility of

Correspondence: Rufus A. Johnstone, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.
Tel.: +44 1223 336685; fax: +44 1223 336676;
e-mail: raj1003@hermes.cam.ac.uk

one-sided partner control by means of an exit threat, and this possibility was recently experimentally verified in the case of the cleaner–client mutualism – Bshary & Grutter (2005) showed that cleaners may be induced to feed on less preferred food items in response to the threat of removal of the food. This form of control, however, depends on the assumption that a victim who escapes cannot immediately be replaced, as the exit threat is only effective if early termination of an encounter imposes some cost on the exploiter. As the power of the 'exit threat' as a means of partner control thus depends on the relative abundance of exploiters and victims (for instance, of cleaners and clients), the interaction between two individuals forms part of a biological market (Noë *et al.*, 1991; Noë & Hammerstein, 1994; Noë, 2001).

Noë & Hammerstein (1994) contrasted the central theme of market models, supply and demand, with the central theme of most models of cooperation, 'partner verification' or (in other words) the control of cheating. While arguing that cooperative systems in which cheating plays an insignificant role are more common than systems in which partner verification is a major problem, they suggested that it might be important to treat cheating and market mechanisms simultaneously in future models. Ferrière *et al.* (2002) took an important step in this direction, demonstrating that when cheats suffer in competition with more cooperative individuals for commodities provided by mutualistic partners, selection can maintain cooperation (and see Ferriere *et al.* 2007). However, in their analysis, the competitive disadvantage that cheats suffer is exogenously imposed; they do not explicitly consider the processes of partner verification that give rise to this effect. Here, we provide a model of mutualistic interaction in which we focus explicitly on the control of cheating by means of the threat of departure, and explore the impact of market supply and demand on this form of partner control.

We extend the simple model of Johnstone & Bshary (2002) to explore the interplay between market forces and control over the duration of encounters, and how these factors influence the behaviour of both exploiters and victims and the net pay-offs that both classes of individuals can expect to obtain from their interaction. Bshary & Noë (2003) predicted that partner choice on the part of potential victims would act very generally to stabilize mutualistic relationships (and see Sachs *et al.*, 2004; Foster & Wenseleers, 2006), and although our analysis is loosely modelled on the cleaner–client mutualism, it is potentially applicable to many forms of intraspecific cooperation and interspecific mutualism in which partners exhibit a similar asymmetry in their strategic options. Classical examples in which exit threats have been proposed to stabilize cooperative behaviour include cooperative breeding based on 'pay-to-stay' (Reeve, 1992; Mulder & Langmore, 1993; Balshine-Earn *et al.*, 1998; Bergmuller & Taborsky, 2005; Bergmuller *et al.*, 2005; Stiver *et al.*, 2005), some plant–seed predator mutualisms (Addicott *et al.*, 1990; Dufay & Anstett, 2003) and plant–rhizobia interactions (Herre *et al.*, 1999; Kiers *et al.*, 2003).

A model of partner control in an asymmetric encounter

Consider two populations, one of potential exploiters (cleaners) and one of potential victims (clients). Members of each population engage in sequential, pairwise interactions with randomly chosen members of the other, over a period of time that is long compared with the duration of any one encounter. Thus, cleaners alternate between 'time in' during which they are interacting with a client, and 'time out' during which they are searching for a new, available client. Similarly, clients alternate between 'time in' during which they are interacting with a cleaner, and 'time out' during which they are searching for a new, available cleaner.

The pay-offs to a cleaner/client pair from a single interaction depend upon the level of exploitation (biting of live tissue) by the cleaner, x, and on the duration of the interaction, t. We treat each encounter as a sequential game, in which the cleaner chooses at what level to exploit, and the potential victim chooses the duration of interaction in response. In the absence of exploitation (i.e. when $x = 0$), both players derive a benefit $b(t)$ from the encounter (the client because of removal of its parasites, the cleaner because of the food they provide); the longer the interaction, the greater the benefit, (i.e. b is an increasing function of t), but the returns to be gained are finite and diminish with time. We shall assume, following Johnstone & Bshary (2002), that $b(t) = 1 - e^{-t/k}$. Here, k is a parameter that determines the shape of the benefit function. A low value of k indicates that the mutualistic benefits of interaction diminish rapidly (in the case of a cleaner/client interaction, perhaps because the client's parasite load is low), whereas a high value of k indicates that the benefits diminish more slowly. Formally, the time taken to acquire any given fraction of the total possible benefit is inversely proportional to k.

Exploitation imposes an additive cost on the victim, and confers an additive benefit on the perpetrator, both proportional to xt, the product of the exploitation level and the duration of interaction. Quantifying exploitation in terms of the damage inflicted on the victim, we shall assume that the cost is equal to xt, and the benefit to cxt, where the parameter c determines the reward gained per unit cost inflicted (we might think of this as the 'temptation to cheat'; a high value of c indicates that the rewards of exploitation are large relative to the costs imposed on the victim).

While searching, a cleaner or a client encounters available potential partners at a rate proportional to their availability, the constant of proportionality being denoted a_e for cleaners (exploiters) and a_v for clients (victims). As encounters are random, the duration of a period of time out follows a negative exponential probability distribution, so that its mean (average search time) is simply the inverse of encounter frequency. Our measure of fitness in this population setting is the long-term average rate of gain that an individual obtains (assuming that the pay-off from any one interaction is as specified above).

Calculating search times and rates of gain

Consider a population in which cleaners exploit at level $\hat{x}$, and clients allow their interactions to continue for time $\hat{t}$. We first calculate the average time out (search time) for cleaners and clients in this population, denoted $s_e(\hat{t})$ and $s_v(\hat{x})$ respectively. To do so, we note that an individual cleaner encounters available clients at a rate proportional to their density, but that this density depends on the average length of time out vs. time in for clients, as this determines the proportion that is searching for cleaners at any given moment. Equally, an individual client encounters available cleaners at a rate proportional to their density, but this density depends on the average length of time out vs. time in for cleaners, as this determines the proportion that is searching for clients at any given moment. $s_e(\hat{t})$ and $s_v(\hat{x})$ are thus jointly defined by the simultaneous equations.

$$s_e(\hat{t}) = \frac{1}{a_e}\frac{\hat{t} + s_v}{s_v}, \quad s_v(\hat{t}) = \frac{1}{a_v}\frac{\hat{t} + s_e}{s_e} \tag{1}$$

(implying that search time equals the inverse of encounter rate, which is given by the appropriate constant of proportionality multiplied by the fraction of time that potential partners spend searching rather than interacting). These equations yield the solution

$$\begin{aligned} s_e(\hat{t}) &= \frac{1 + a_v\hat{t} - a_e\hat{t} + \sqrt{1 + 2(a_e + a_v)\hat{t} + (a_e - a_v)^2\hat{t}^2}}{2a_e}, \\ s_v(\hat{t}) &= \frac{1 + a_e\hat{t} - a_v\hat{t} + \sqrt{1 + 2(a_e + a_v)\hat{t} + (a_e - a_v)^2\hat{t}^2}}{2a_v} \end{aligned} \tag{2}$$

Having derived the mean time out for cleaners and clients, we can easily determine the fitness of individuals of both types in our population, measured as their long-term average rate of gain, which we denote $\hat{w}_e(\hat{x}, \hat{t})$ and $\hat{w}_v(\hat{x}, \hat{t})$

$$\begin{aligned} \hat{w}_e(\hat{x}, \hat{t}) &= \frac{1 - \exp(-\hat{t}/k) + c\hat{x}\hat{t}}{\hat{t} + s_e(\hat{t})}, \\ \hat{w}_v(\hat{x}, \hat{t}) &= \frac{1 - \exp(-\hat{t}/k) - \hat{x}\hat{t}}{\hat{t} + s_v(\hat{t})} \end{aligned} \tag{3}$$

Solving for the ESS

Our population strategy pair $(\hat{x}, \hat{t})$ represents an ESS if an individual cleaner or client that adopts a different level of exploitation or allows an interaction to continue for a different length of time cannot enjoy as great an average rate of gain as a typical individual.

The optimal time for which a client in this population should allow an interaction to continue, given that the cleaner with whom it is interacting exploits at any given level x, which we denote $t_{\mathrm{opt}}(x; \hat{x}, \hat{t})$, can easily be determined through the application of the marginal value theorem. The client should allow the interaction to continue until the marginal value of continued interaction is precisely equal to the marginal opportunity cost, or, in other words, to its long-term average rate of gain in this population, $\hat{w}_v(\hat{x}, \hat{t})$. Formally,

$$\frac{1}{k}\exp\left[-\frac{t_{\mathrm{opt}}(x; \hat{x}, \hat{t})}{k}\right] - x = \hat{w}_v(\hat{x}, \hat{t}) = \frac{1 - \exp(\hat{t}/k) - \hat{x}\hat{t}}{\hat{t} + s_v(\hat{t})} \tag{4}$$

where the left-hand term in the above equation represents the marginal value of continued interaction at time $t_{\mathrm{opt}}(x; \hat{x}, \hat{t})$, and the right-hand term the long-term average rate of gain. This yields

$$\begin{aligned} t_{\mathrm{opt}}(x; \hat{x}, \hat{t}) = {} & k\log[s_v(\hat{t}) + \hat{t}] - k\log[k(1 - \exp(-\hat{t}/k) \\ & + s_v(\hat{t})x + \hat{t}(x - \hat{x}))] \end{aligned} \tag{5}$$

Given our assumption that the potential victim can determine the length of interaction, our first requirement for an ESS is therefore

$$\hat{t} = t_{\mathrm{opt}}(\hat{x}; \hat{x}, \hat{t}) \tag{6}$$

implying that the population duration of interaction is optimal (given the population level of exploitation). We can also see from eqn 5 that t_{opt} decreases with x, so that greater levels of exploitation by a cleaner favour earlier termination of interaction by a client, but that (assuming the client gains something from the interaction) t_{opt} increases with $s_v(\hat{t})$, implying that the client should be willing to tolerate a longer interaction for any given level of exploitation if it takes longer to find a replacement partner. Having determined the optimal response on the part of clients to a cleaner that exploits at different intensities, we can also determine the long-term average rate of gain of a cleaner in this population that exploits at level x (assuming that clients respond optimally to any change in the level of exploitation by a cleaner), denoted $w_e(x; \hat{x}, \hat{t})$. This is given by

$$w_e(x; \hat{x}, \hat{t}) = \frac{1 - \exp[-t_{\mathrm{opt}}(x; \hat{x}, \hat{t})/k] + cxt_{\mathrm{opt}}(x; \hat{x}, \hat{t})}{t_{\mathrm{opt}}(x; \hat{x}, \hat{t}) + s_e(\hat{t})} \tag{7}$$

Our second requirement for an ESS is therefore

$$w_e(\hat{x}; \hat{x}, \hat{t}) > w_e(x; \hat{x}, \hat{t}) \quad \text{for all } x \neq \hat{x} \tag{8}$$

implying that

$$\frac{\partial w_e(x; \hat{x}, \hat{t})}{\partial x} = 0 \quad \text{for } x = \hat{x} \tag{9}$$

Joint solution of eqns 6 and 9 then yields an ESS strategy pair. Unfortunately, we are unable to obtain an analytical solution to these equations; numerical results for representative parameter values are, however, presented in the next section.

Incomplete control of the duration of interaction

We can extend the model to allow for incomplete control by the victim over the length of the encounter (as a cleaner, for instance, may be able to pursue a client or otherwise hinder escape). To do so, we assume that the interaction will not terminate at the victim's optimal endpoint. Rather, it will continue until the net marginal costs of prolonged interaction to the victim exceed some critical threshold relative to the net marginal benefits of prolonged interaction to the exploiter. Only at this point, we assume, will the former be willing to make sufficient efforts to escape the latter. The threshold ratio of costs to benefits depends upon the relative control that each player can exercise over the duration of encounter; we will assume that it is equal to $s/(1-s)$, where the parameter s (which ranges from 0 to 1) represents the relative 'power' of the exploiter. $s = 0$ implies that the potential exploiter has no influence over departure, so that the interaction finishes at the optimal time for the potential victim; greater values of s imply that the exploiter has greater ability to prolong the interaction (and for a sufficiently large value of s may be able to do so indefinitely); $s = 1$ indicates that the potential exploiter has full control.

Given the above assumptions, the duration of interaction for a given level of exploitation, x, and exploiter 'power' s, denoted $\tilde{t}(x;\hat{x},\hat{t};s)$, satisfies

$$\begin{aligned} -\left[\frac{1}{k}\exp\left(-\frac{\tilde{t}(x;\hat{x},\hat{t};s)}{k}\right)-x\right]+\left[\frac{1-\exp(-\hat{t}/k)-\hat{x}\hat{t}}{\hat{t}+s_{\mathrm{v}}(\hat{t})}\right] \\ =\frac{s}{1-s}\left\{\left[\frac{1}{k}\exp\left(-\frac{\tilde{t}(x;\hat{x},\hat{t};s)}{k}\right)+cx\right]\right. \\ \left.-\left[\frac{1-\exp(-\hat{t}/k)+c\hat{x}\hat{t}}{\hat{t}+s_{\mathrm{e}}(\hat{t})}\right]\right\} \end{aligned} \tag{10}$$

where the left-hand side of the above equation represents the net marginal cost of continued interaction for the client (i.e. the difference between the marginal benefit of continued interaction and the marginal opportunity cost, which is equal to the long-term average rate of gain in the population), and the right-hand side $[s/(1-s)]$ times the net marginal pay-off to continued interaction for the cleaner. This yields

$$\tilde{t}(x;\hat{x},\hat{t};s)=k\ln\left[\frac{1}{k}\frac{(1-2s)[\hat{t}+s_{\mathrm{v}}(\hat{t})]}{\{1+x[\hat{t}+s_{\mathrm{v}}(\hat{t})]-s[2+(1-c)[xs_{\mathrm{v}}(\hat{t})+(x-\hat{x})\hat{t}]]-\hat{x}\hat{t}\}-(1-2s)\mathrm{e}^{-\hat{t}/k}}\right] \tag{11}$$

which reduces, in the special case of $s = 0$ (implying complete control by the victim), to the expression for $t_{\mathrm{opt}}(x;\hat{x},\hat{t})$ given in eqn 5.

We can then re-derive the long-term average rate of gain of a cleaner that exploits at level x, allowing for incomplete control over the duration of interaction, which we denote $\tilde{w}_{\mathrm{e}}(x;\hat{x},\hat{t};s)$. This is given by

$$\tilde{w}_{\mathrm{e}}(x;\hat{x},\hat{t};s)=\frac{1-\exp[-\tilde{t}(x;\hat{x},\hat{t};s)/k]+cx\tilde{t}(x;\hat{x},\hat{t};s)}{\tilde{t}(x;\hat{x},\hat{t};s)+s_{\mathrm{e}}(\hat{t})} \tag{12}$$

Our ESS conditions in the extended model are then

$$\hat{t}=\tilde{t}(\hat{x};\hat{x},\hat{t};s) \tag{13}$$

and

$$\tilde{w}_{\mathrm{e}}(\hat{x};\hat{x},\hat{t};s)>\tilde{w}_{\mathrm{e}}(x;\hat{x},\hat{t};s)\quad\text{for all } x\neq\hat{x} \tag{14}$$

implying that

$$\frac{\partial\tilde{w}_{\mathrm{e}}(x;\hat{x},\hat{t};s)}{\partial x}=0\quad\text{for } x=\hat{x} \tag{15}$$

Once again, we are unable to obtain an analytical solution to these equations; but numerical results for representative parameter values are again presented in the Results section.

Results

We focus on the impact of: (1) the benefits to be gained by exploitation; and (2) the relative abundance of exploiters vs. victims, on the solution of the model. Figures 1 and 2 show the stable level of exploitation, and the corresponding duration of interaction, as a function of c, the 'temptation to cheat' and $\log_2(a_{\mathrm{e}}/a_{\mathrm{v}})$, the log of the ratio of encounter rates for cleaners compared with clients, assuming that $k = 1$ and $a_{\mathrm{v}} + a_{\mathrm{e}} = 1$. As encounter rates are proportional to the availability of potential partners, the latter assumption implies that the total combined abundance of cleaners and clients remains constant, while we vary the ratio of clients to cleaners – positive values of the ratio $\log_2(a_{\mathrm{e}}/a_{\mathrm{v}})$ imply that clients are more abundant than cleaners, and that cleaners therefore encounter potential partners more frequently, whereas negative values imply that clients are less abundant than cleaners, and that cleaners therefore encounter potential partners less frequently.

The graphs reveal that as the temptation to cheat grows, exploitation by cleaners increases, and the duration of interaction correspondingly decreases (because of clients terminating their encounters earlier). The outcome of the model is also, however, strongly influenced by the relative abundance of potential exploiters and potential victims. When clients are abundant and

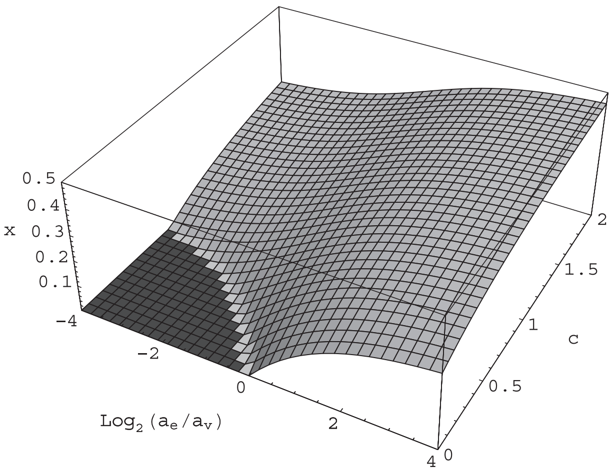

Fig. 1 The stable level of exploitation (x), in the basic model in which clients control the duration of interaction, as a function of the log of the ratio of client-to-cleaner abundance [$\log_2(a_e/a_v)$], and the 'temptation to cheat' (c), assuming that $k = 1$ and $a_e + a_v = 1$. The region in which exploitation is not favoured (i.e. $x = 0$) is shaded.

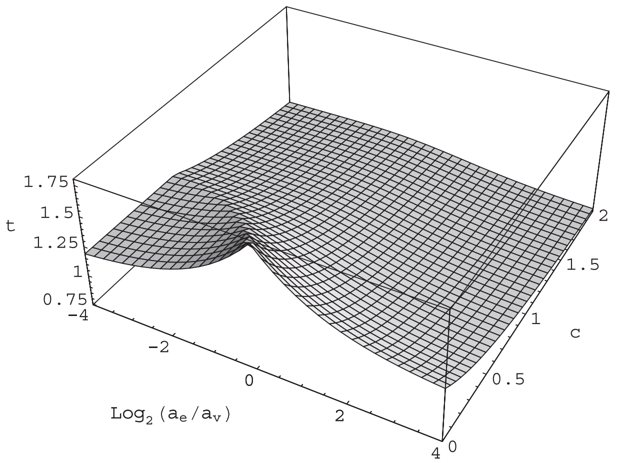

Fig. 2 The stable duration of interaction (t), in the basic model in which clients control the duration of interaction, as a function of the log of the ratio of client-to-cleaner abundance [$\log_2(a_e/a_v)$], and the 'temptation to cheat' (c), assuming that $k = 1$ and $a_e + a_v = 1$.

cleaners rare, cleaners can afford to behave in an exploitative manner, even though this induces clients to terminate their interactions relatively early. As the relative abundance of clients decreases, however, the stable level of exploitation declines and clients allow their interactions to continue longer. When clients are less abundant than cleaners [and $\log_2(a_e/a_v) < 0$], we see that there is even a critical level of temptation (i.e. a critical value of c) below which cleaners do best to completely forego the opportunity for exploitation (i.e. the stable level of exploitation is zero). Under these circumstances, clients terminate their interactions earlier than is in the best interest of cleaners, and the benefits of exploitation to a cleaner are outweighed by the costs of shortening its encounters still further.

When the stable level of exploitation drops to zero, and it is the clients that terminate interaction, the duration of encounters declines as the relative abundance of clients decreases, as it is easier for clients to find a new cleaner when the latter are relatively more abundant. This gives rise to the 'peak' in encounter duration visible in Fig. 2 at intermediate relative abundance (when the temptation to cheat is low) – above the peak, encounters are terminated by exploitative cleaners, and interaction duration increases as clients become relatively less abundant; below the peak, there is no exploitation and encounters are terminated by clients; so, interaction duration decreases as clients become relatively less abundant (and cleaners relatively more abundant).

The key factor driving the effects described above is the changing costs of partner replacement for clients vs. cleaners, which are illustrated in Fig. 3. The graphs show the time required by both types to find a replacement partner (s_v and s_e) at equilibrium, again as a function of c, the 'temptation to cheat' and $\log_2(a_e/a_v)$, the log of the ratio of encounter rates for cleaners compared with clients. They confirm that as the relative abundance of cleaners decreases, the time they require to find a replacement partner shrinks, whereas the time clients require to find a replacement partner increases. This explains why cleaners can afford to exploit their victims more intensely under these circumstances, despite the fact that this causes their victims to terminate the interaction earlier.

Figure 4, which shows the optimal termination time from the client's perspective (in a population that adopts the stable strategy pair) as a function of the level of exploitation by an individual cleaner, for several different values of $\log_2(a_e/a_v)$, also confirms that as the relative abundance of cleaners decreases, clients should be prepared to tolerate a given level of exploitation longer because of the increased time required to find a replacement partner. As Fig. 2 shows, however, stable interaction time nevertheless decreases despite this greater tolerance, because of the increase in the stable level of exploitation.

When clients lack complete control over the duration of encounters, cleaners may exploit at higher rates (as, for a given level of exploitation, they are able to maintain their interactions for a longer time). This is illustrated in Fig. 5, which shows the stable level of exploitation as a function of s (the extent of cleaner influence on the duration of interaction), for different ratios of client-to-cleaner abundance and for different levels of temptation to cheat. In all cases, exploitation increases with cleaner control, rising rapidly and indefinitely as s approaches some critical value; above this threshold, clients are simply unable to escape, so that there is nothing (given the simple assumptions of our model) to

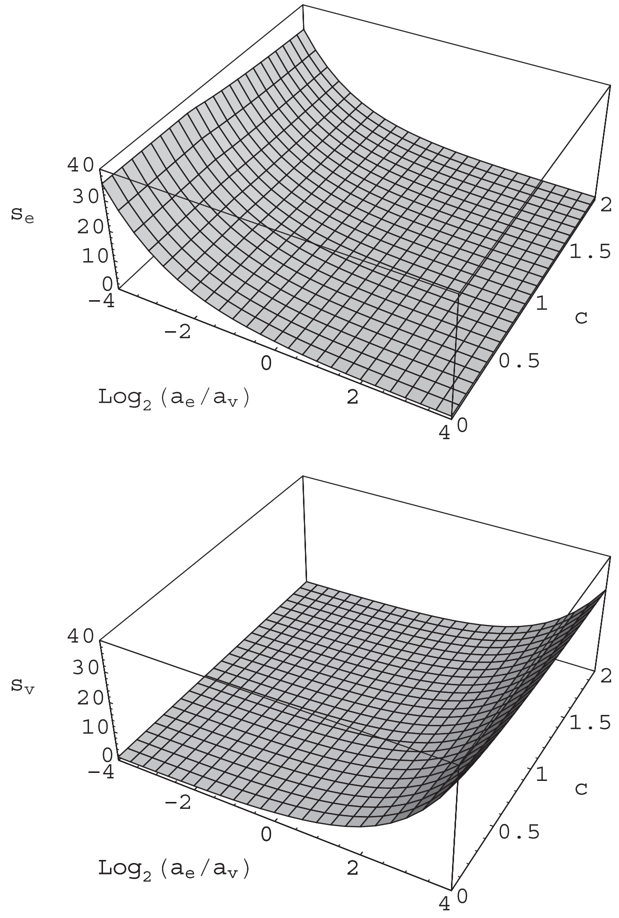

Fig. 3 The mean time required to find a replacement partner for cleaners (upper graph) and for clients (lower graph) at equilibrium, in the basic model in which clients control the duration of interaction, as a function of the log of the ratio of client-to-cleaner abundance [$\log_2(a_e/a_v)$], and the 'temptation to cheat' (c), assuming that $k = 1$ and $a_e + a_v = 1$.

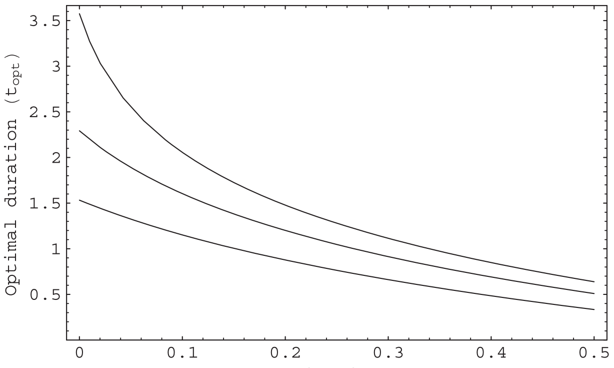

Fig. 4 The optimal duration of interaction (from the client's perspective), as a function of a cleaner's level of exploitation, in a population adopting the stable strategy pair. Successively higher curves correspond to higher ratios of client-to-cleaner abundance [$\log_2(a_e/a_v) = -2$, 0 and 2]. In all cases, $k = 1$, $a_e + a_v = 1$ and $c = 1$.

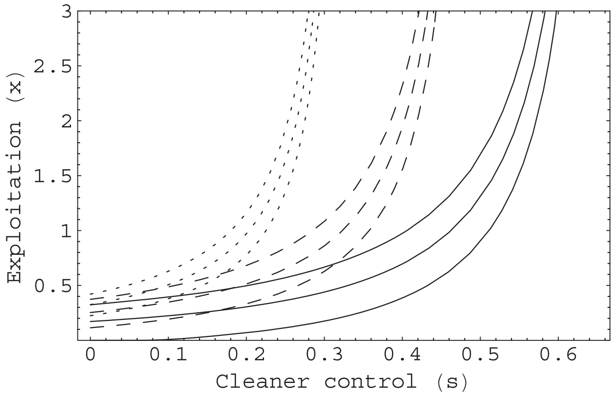

Fig. 5 The stable level of exploitation (x), as a function of s, the extent of cleaner influence on the duration of interaction, for three different values of the log of the ratio of client-to-cleaner abundance [$\log_2(a_e/a_v)$] and three different values of the 'temptation to cheat' (c), assuming that $a_e + a_v = 1$. Solid curves give results for $c = 0.5$, long-dashed curves for $c = 1$ and short-dashed curves for $c = 2$. In each set, successively lower curves correspond to successively lower values of [$\log_2(a_e/a_v)$], respectively, 2, 0 and −2.

prevent unlimited exploitation (see Johnstone & Bshary, 2002). The threshold is attained more readily when cleaners are rare and have a stronger temptation to cheat. However, these factors have a more pronounced effect at lower values of s, as the threat of termination is stronger under these circumstances.

Even if cleaners cannot entirely prevent clients from escaping, if they have sufficient influence over the duration of interaction, they will be able to exploit at a high enough rate for long enough that clients actually incur a net cost as a result of their interaction; in other words, the relationship between cleaners and clients has shifted from mutualism to exploitation and parasitism. Figure 6 shows that this switch occurs when cleaner control (measured by the parameter s) exceeds some critical level (less than that required for unlimited exploitation), which depends upon the 'temptation to cheat' and the relative abundance of clients vs. cleaners. The greater the potential benefits of exploitation, and the greater the relative abundance of clients, the more readily the relationship slides into parasitism (i.e. client pay-offs drop below zero at a lower value of s under these circumstances).

Discussion

In a previous analysis of exit threats as a means of partner control in asymmetric interactions (Johnstone & Bshary, 2002), we focused on a single interaction between a potential exploiter and a potential victim, and assumed that the latter would (when capable of doing so) terminate the encounter at the point where the diminishing marginal benefits of continued interaction dropped below the marginal cost of continued

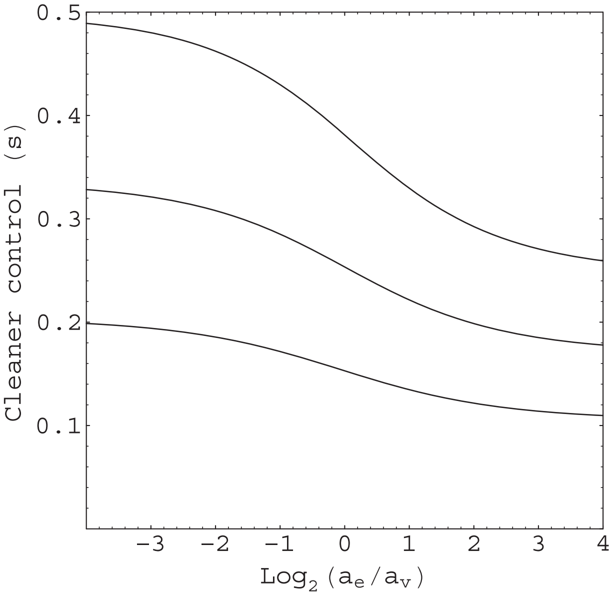

Fig. 6 Range of values of [$\log_2(a_e/a_v)$], log ratio of client-to-cleaner abundance, and s, extent of cleaner influence on the duration of interaction, over which clients obtain positive vs. negative pay-offs. Towards the lower left, pay-offs are positive; towards the upper right, pay-offs are negative. Successively higher curves correspond to the boundary between positive and negative pay-offs for successively smaller values of c, the 'temptation to cheat', respectively, 2, 1 and 0.5. In all cases, $k = 1$ and $a_e + a_v = 1$.

exploitation. Here, we have set such encounters in a market context, assuming that victims (when capable) terminate an encounter at the point where the net marginal benefits of continued interaction drop below the victim's long-term average rate of gain. In other words, we take into account the opportunity cost of continuing to interact with one partner. When fresh interactions offer the possibility of a greater rate of gain, it may thus pay a potential victim to leave, even though the net marginal benefit of continued interaction is still positive relative to the outside option of not interacting at all. One might view this as an application of optimal foraging theory, in which we treat each potential exploiter as a patch yielding diminishing returns, and determine the optimal patch residence time for potential victims that will maximize their long-term average rate of gain.

Market effects

It is a familiar result from foraging theory that the optimal duration of patch residence increases with interpatch travel time (Stephens & Krebs, 1986). Similarly, as we have shown here, the optimal duration of encounter from the potential victim's point of view increases, for a given level of exploitation, as the relative abundance of potential exploiters declines, because the interencounter interval then grows longer. In the context of cleaner–client interactions, for instance, the model predicts that clients will tolerate greater levels of exploitation for longer durations before terminating an encounter, when they are abundant relative to cleaners, because the mean time required to find a replacement cleaner is then greater.

The above trend means that potential exploiters can afford to inflict greater costs on victims when the former are relatively less abundant, as doing so will not lead to such early termination by the victims under these circumstances. In addition, potential exploiters themselves will be influenced by the availability of replacement partners. As relative exploiter abundance declines, not only do partners become more tolerant as long as they receive net benefits, but also the costs of victim departure for an exploiter also decrease, as the time required to find a new victim diminishes. This reinforces the selection for higher levels of exploitation under these conditions. Indeed, when relative exploiter abundance is sufficiently low, the optimal duration of interaction may actually be lower for an exploiter than for a victim, despite the fact that the former enjoys not only the mutualistic benefits of interaction (as does the latter), but also the benefits of exploitation. Under these circumstances, exploitation can be favoured not only as a source of immediate benefit, but also as a means to influence interaction length. Inspecting Fig. 1, for instance, we see that 'exploitation' can be favoured even when the temptation to cheat $c = 0$, implying that exploiters gain no immediate benefit by inflicting costs on their victims. This occurs whenever exploiters are less abundant than victims, because the optimal duration of encounter for the former is then shorter than for the latter, so that imposition of costs on a victim serves to induce it to terminate an interaction sooner.

Comparison with previous models

A striking aspect of our results, in contrast to previous market models like the veto game (Kahan & Rapoport 1984), is that they feature a smooth, gradual change in the intensity of exploitation as the ratio of exploiters to victims alters. The first biological market model by Noë & Hammerstein (1994) predicts a full switch between two potential strategies at some critical ratio of the relative abundance of two trading classes, above which the more common class will be forced to offer greater benefits to potential partners. In part, this merely reflects the simplifying assumption in previous models that individuals face the binary choice to offer high or low quality services. However, more significantly, it is also because of the treatment of partner choice as a binary decision. The decision to accept or reject a potential partner is, of necessity, an all-or-nothing one. By contrast, we have focused on the time at which a potential victim should terminate an encounter it has already initiated. This very simple form of control does not require any ability to assess the value of a partner in advance, as the decision is based on benefits and costs actually experienced; more significantly, it also permits continuous variation in response, selecting for a continuous shift in the intensity of exploitation.

Potential for testing in the cleaner–client system

Although there are always more clients than cleaners in coral reefs, most clients do not seek cleaning at any moment in time (Grutter, 1997). What need to be evaluated in future empirical tests of the model are thus changes in the operational cleaner-to-client ratio, analogous to the operational sex ratio (Emlen & Oring, 1977) in mating markets. Currently, we only know that clients often terminate interactions in response to cleaner fish cheating (Bshary & Grutter, 2002; Bshary & Schäffer, 2002). The cleaning system involving the well-studied cleaner species *L. dimidiatus* is further complicated by the fact that clients may actively punish cleaners, may switch to a different cleaner for their next inspection, and may even avoid cleaners that they observed cheating another client (Bshary & Grutter, 2005, 2006). Therefore, a more suitable study species to test predictions of our model would be the closely related cleaner wrasse *Labroides bicolor*, which lacks refined cleaning stations, but roves over large areas (Randall, 1958).

Applicability to other systems

Our model is not relevant only to the cleaner–client mutualism, but also to any interaction in which cooperation is maintained by the threat of sanctions (Herre *et al.*, 1999) of some form. Whereas our model assumes that clients visit cleaners sequentially, the same issues arise when a potential victim interacts with multiple potential exploiters at the same time. Such a situation exists in the mutualism between yucca plants and the seed-predating pollinator, the yucca moth (Addicott *et al.*, 1990; Pellmyr & Huth, 1994; for the senita cactus-moth system, see Fleming & Holland, 1998). The moth female actively pollinates the flowers and oviposits into the developing fruits. The hatching larvae eat the seeds. If there are too many larvae in a fruit, the plant aborts it; this corresponds to the termination of interaction in our model, as it leads to a loss of potential mutualistic benefits by the larvae, as well as a loss of the opportunity for further exploitation. In the absence of partner choice, many eggs could be laid in a fruit by the pollinator. Where a plant has many fruits, however, our model suggests that it might lower the threshold number of larvae likely to trigger abortion, as proposed verbally by Noë *et al.* (1991), because resources can be more easily re-allocated to other developing fruits. In other words, if there are many pollinators on the market, it may pay them to lower their level of exploitation (the number of eggs laid) to increase the duration of the interaction (necessary for successful hatching of the next pollinator generation).

Another potential example suggested by Noë *et al.* (1991) to which the logic of our model applies is the contribution of unrelated helpers in cooperatively breeding species. One reason why unrelated individuals might help to raise the offspring of breeders is to avoid eviction from the territory (Gaston, 1978). This ‘pay-to-stay’ hypothesis was modelled by Hamilton & Taborsky (2005). They found that if considered in isolation, ‘helpers’ impose net costs on breeders. However, the ratio of helpers to breeders on the market determines how easily a helper is replaced and therefore how much it has to invest to be allowed to remain in a breeder’s territory. In a re-analysis of data on pied kingfisher published by Reyer (1986), Noë *et al.* (1991) found that the contribution of a helper relative to the breeders increased with the number of helpers present. In line with the interpretation of these results by Noë *et al.* (1991), our model suggests that a paucity of territories may push helpers’ investment to levels that yield net benefits to breeders because it allows for easier ‘replacement’ of a lazy helper.

Possible extensions

The present model makes a number of assumptions that might be modified or relaxed in future analyses. In particular, we have assumed that the returns on cooperation diminish with time in the same manner [specified by the benefit function, $b(t)$] for both parties, and that these are independent of an individual’s past history of interaction. In reality, however, it may sometimes be the case that one party in an encounter can continue to enjoy benefits from interaction beyond the point at which (in the absence of exploitation) there is anything to be gained for the other. In the case of cleaner fish–client interactions, the assumption that the benefits of cooperation diminish at the same rate for both parties is reasonable to the extent that this decrease is the result of the reduction in the parasite load of the client. As the parasite load is reduced, there is less for the cleaner to eat without biting client tissue – i.e. engaging in exploitation – and for the same reason less for the client to gain from the cleaner’s attentions. If, however, the potential benefits to the cleaner decrease because of satiation, then the benefit function is likely to differ for cleaners and clients (as the latter benefit from parasite removal regardless of how hungry the client is). In addition, if temporary satiation of the cleaner is important, we might also suppose that the potential benefits of exploitation (or, equivalently, the cost inflicted on the client for a given level of exploitative benefit obtained by the cleaner) change over time.

As regards the second assumption we emphasized above, it is certainly possible that the benefits to be gained from an encounter will depend upon the time since an individual last engaged in an interaction (as well as its duration). If a client, for example, has its parasite load reduced by a cleaner, then it may have little to gain from a new interaction until this load has built up once again. If cleaners can become satiated, an equivalent argument applies to them also. By contrast, we have assumed that each new interaction offers the same, initially high rate of gain. This assumption is acceptable if there is sufficient delay between interactions for individuals to return to their baseline state, but may be problematic when encounters are very frequent. Unfortunately, however, to model optimal behaviour, when the benefits of cooperation depend on past history, would require a state-dependent approach (see Houston & McNamara, 1999) that is likely to prove less tractable than our current analysis.

Conclusions

In general, our model shows that the threat of terminating interaction, while it can serve to suppress cheating under some circumstances, is highly sensitive to market forces. As this is a simple, and probably widespread form of control, especially in asymmetric interactions (Schuessler, 1989; Hauk, 2001; West *et al.*, 2002; Frank, 2003; Sachs *et al.*, 2004; Cant & Johnstone 2006; Foster & Wenseleers, 2006), our results argue for the general importance of markets in the maintenance of cooperation, supporting the various empirical studies in which market forces have been found to influence pay-off distributions (Noë, 1990; Schwartz & Hoeksema 1998; Wilkinson, 2001; Bshary & Grutter, 2002; Henzi & Barrett, 2002; Simms & Taylor 2002).

Acknowledgments

This research was supported by NERC grant NER/A/S/2002/00898 (RAJ and RB) and by the Swiss Science Foundation (RB).

References

Addicott, J.F., Bronstein, J.L. & Kjellberg, F. 1990. Evolution of mutualistic life cycles: Yucca moths and fig wasps. In: *Genetics, Evolution, and Coordination of Insect Life Cycles* (F. Gilbert, ed.), pp. 143–161. Springer-Verlag, London.

Balshine-Earn, S., Neat, F., Reid, H. & Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping in a cooperatively breeding fish. *Behav. Ecol.* **9**: 432–438.

Bergmuller, R. & Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers 'pay-to-stay' by pre-emptive appeasement. *Anim. Behav.* **69**: 19–28.

Bergmuller, R., Heg, D., Peer, K. & Taborsky, M. 2005. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proc. R. Soc. Lond. B* **272**: 325–331.

Bshary, R. 2001. The cleaner fish market. In: *Economics in Nature* (R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein, eds), pp. 146–172. Cambridge University Press, Cambridge.

Bshary, R. & Bronstein, J.L. 2004. Game structures in mutualisms: what can the evidence tell us about the kind of models we need? *Adv. Stud. Behav.* **34**: 59–101.

Bshary, R. & Grutter, A.S. 2002. Experimental evidence that partner choice is the driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. *Ecol. Lett.* **5**: 130–136.

Bshary, R. & Grutter, A.S. 2005. Punishment and partner choice cause cooperation in a cleaning mutualism. *Biol. Lett.* **1**: 396–399.

Bshary, R. & Grutter, A.S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature*, **441**: 975–978.

Bshary, R. & Noë, R. 2003. Biological markets: the ubiquitous influence of partner choice on cooperation and mutualism. In: *Genetic and Cultural Evolution of Cooperation* (P. Hammerstein, ed.), pp. 167–184. MIT Press, Cambridge, MA.

Bshary, R. & Schäffer, D. 2002. Choosy reef fish select cleaner fish that provide high service quality. *Anim. Behav.* **63**: 557–564.

Cant, M.A. & Johnstone, R.A. 2006. Self-serving punishment and the evolution of cooperation. *J. Evol. Biol.* **19**: 1383–1385.

Côté, I.M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanorg. Mar. Biol.* **38**: 311–355.

Dufay, M. & Anstett, M.-C. 2003. Conflicts between plants and pollinators that reproduce within inflorescences: Evolutionary variations on a theme. *Oikos* **100**: 3–14.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**: 215–223.

Ferrière, R., Bronstein, J.L., Rinaldi, S., Law, R. & Gauduchon, M. 2002. Cheating and the evolutionary stability of mutualisms. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **269**: 773–780.

Ferriere, R., Gauduchon, M. & Bronstein, J.L. 2007. Evolution and persistence of obligate mutualists and exploiters: competition for partners and evolutionary immunization. *Ecol. Lett.* **10**: 115–126.

Fleming, T.H. & Holland, J.N. 1998. The evolution of obligate pollination mutualisms: senita cactus and senita moth. *Oecologia* **114**: 368–375.

Foster, K.R. & Wenseleers, T. 2006. A general model for the evolution of mutualisms. *J. Evol. Biol.* **19**: 1283–1293.

Frank, S.A. 2003. Perspective: repression of competition and the evolution of cooperation. *Evolution* **57**: 693–705.

Gaston, A.J. 1978. The evolution of group territorial behaviour and cooperative breeding. *Am. Nat.* **112**: 1091–1100.

Grutter, A.S. 1997. Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia*, **1997**: 346–355.

Grutter, A.S. & Bshary, R. 2003. Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proc. R. Soc. Lond. B* **270**(Suppl.): 242–244.

Hamilton, I.M. & Taborsky, M. 2005. Unrelated helpers will not fully compensate for costs imposed on breeders when they pay to stay. *Proc. R. Soc. Lond. B* **272**: 445–454.

Hauk, E. 2001. Leaving the prisoner's dilemma: permitting partner choice and refusal in prisoner's dilemma games. *Comp. Econ.* **18**: 65–87.

Henzi, S.P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Anim. Behav.* **63**: 915–921.

Herre, E.A., Knowlton, N., Mueller, U.G. & Rehner, S.A. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* **14**: 49–53.

Houston, A.I. & McNamara, J. 1999. *Models of Adapative Behaviour*. Cambridge University Press, Cambridge.

Johnstone, R.A. & Bshary, R. 2002. From parasitism to mutalism: partner control in asymmetric interactions. *Ecol. Lett.* **5**: 634–639.

Kahan, J.P. & Rapoport, A. 1984. *Theories of coalition formation*. Lawrence Erlbaum Associates, Hillsdale, NJ.

Kiers, E.T., Rousseau, R.A., West, S.A. & Denison, R.F. 2003. Host sanctions and the legume–rhizobium mutualism. *Nature* **425**: 78–81.

Losey, G.C., Grutter, G.S., Rosenquist, G., Mahon, J.L. & Zamzow, J.P. 1999. Cleaning symbiosis: a review. In *Behaviour and conservation of littoral fish* (V.C. Almada, R.F. Oliveira & E.J. Gonclaves, eds), pp. 379–395. Instituto Superior de Psicologia Aplicada, Lisbon.

Mulder, R.A. & Langmore, N.E. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* **45**: 830–833.

Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Anim. Behav.* **39**: 78–90.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of cooperation. In: *Economics in Nature* (R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein, eds), pp. 93–118. Cambridge University Press, Cambridge.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**: 1–11.

Noë, R., van Schaik, C.P. & van Hooff, J.A.R.A.M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology* **87**: 97–118.

Pellmyr, O. & Huth, C.J. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**: 257–260.

Randall, J.E. 1958. A review of the labrid fish genus Labroides, with descriptions of two new species and notes on ecology. *Pac. Sci.* **12**: 327–347.

Reeve, H.K. 1992. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* **358**: 147–149.

Reyer, H.U. 1986. Breeder-helper interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour* **96**: 277–303.

Sachs, J.L., Mueller, U.G., Wilcox, T.P. & Bull, J.J. 2004. The evolution of cooperation. *Q. Rev. Biol.* **79**: 135–160.

Schuessler, R. 1989. Exit threats and cooperation under anonymity. *J. Conflict Resolut.* **33**: 728–749.

Schwartz, M.W. & Hoeksema, J.D. 1998. Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* **79**: 1029–1038.

Simms, E.L. & Taylor, D.L. 2002. Partner choice in nitrogen fixation mutualisms of legumes and rhizobia. *Integrative and Comparative Biology* **42**: 369–380.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.

Stiver, K.A., Dierkes, P., Taborsky, M., Gibbs, H.L. & Balshine, S. 2005. Relatedness and helping in fish: examining the theoretical predictions. *Proc. R. Soc. Lond. B* **272**: 1593–1599.

Trivers, R.L. 1971. Evolution of reciprocal altruism. *Quarterly Review of Biology* **46**: 35-57.

West, S.A., Kiers, E.T., Pen, I. & Denison, R.F. 2002. Sanctions and mutualism stability: when should less beneficial mutualisms be tolerated? *J. Evol. Biol.* **15**: 830–837.

Wilkinson, D.M. 2001. Mycorrhizal evolution. *Trends Ecol. Evol.* **16**: 64–65.

Received 16 October 2007; revised 21 December 2007; accepted 7 January 2008