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Honesty and cheating in cleaning symbioses: evolutionarily stable strategies defined by variable pay-offs

Robert P. Freckleton[1*] and Isabelle M. Côté[2]

[1]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*
[2]*Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK*

Game-theory models have indicated that the evolution of mixed strategies of cheating and honesty in many mutualisms is unlikely. Moreover, the mutualistic nature of interspecific interactions has often been difficult to demonstrate empirically. We present a game-theory analysis that addresses these issues using cleaning symbioses among fishes as a model system. We show that the assumption of constant pay-offs in existing models prevents the evolution of evolutionarily stable mixed strategies of cheating and honesty. However, when interaction pay-offs are assumed to be density dependent, mixed strategies of cheating and honesty become possible. In nature, cheating by clients often takes the form of retaliation by clients against cheating cleaners, and we show that mixed strategies of cheating and honesty evolve within the cleaner population when clients retaliate. The dynamics of strategies include both negative and positive effects of interactions, as well as density-dependent interactions. Consequently, the effects of perturbations to the model are nonlinear. In particular, we show that under certain conditions the removal of cleaners may have little impact on client populations. This indicates that the underlying mutualistic nature of some interspecific interactions may be difficult to demonstrate using simple manipulation experiments.

Keywords: population model; game theory; positive interactions; coral reef

1. INTRODUCTION

Interspecific mutualisms can have far-reaching impacts on individual behaviour and life histories (Holland & Fleming 1999), population dynamics (Stachowicz & Hay 1999) and even large-scale patterns of biodiversity (Van der Heijden *et al.* 1998). Species involved in obligate mutualisms face an intrinsic conflict because each species is under selection for increased exploitation of the other (Axelrod & Hamilton 1981). Theoretical models indicate that this conflict is a source of evolutionary instability, and that evolution of 'cheating' by one party, i.e. receiving the benefits of mutualism but not reciprocating (Boucher *et al.* 1982), may lead to reciprocal extinction (Trivers 1971; Bull & Rice 1991). However, cheating often occurs in obligate mutualisms in nature (e.g. Pellmyr *et al.* 1996; Yu & Pierce 1998; Stanton *et al.* 1999), and cheaters can be present in high proportions in some apparently stable symbioses (Addicott 1996).

Marine cleaning symbioses are a form of mutualism in which a cleaner (usually a small fish or shrimp) removes ectoparasites from the body of a cooperating fish client (Feder 1966). These interactions appear to possess traits that are predicted to buffer such systems against cheating (Trivers 1971; Axelrod & Hamilton 1981; Soberon Mainero & Martinez del Rio 1985). Cleaning (the 'service') and removal of ectoparasites (the 'benefit') occur simultaneously; thus, retaliation by clients against cheating cleaners can be swift. Individual cleaners and clients can also interact repeatedly over the course of their lifetimes;

hence, cheaters may be recognized and avoided (or eaten) (Bshary & Schäffer 2002). Despite this incentive for honesty, cleaners often take not only ectoparasites but also scales, tissue and mucus in large quantities from their clients (reviewed in Côté 2000), which may be deleterious to clients.

Conversely, there is also evidence of both honesty and cheating among clients. Honest clients invite cleaners by adopting ritual immobile postures that give cleaners access to their buccal cavity and gills while generally refraining from consuming them (Côté 2000). However, cleaners have been found in the gut contents of potential clients (Côté 2000), and attempted predation of cleaners by clients has been witnessed (Francini-Filho *et al.* 2000).

In an attempt to model the evolution of cheating and honesty in a cleaner–client system, Poulin & Vickery (1995) found that, under the assumption of fixed pay-offs and penalties, the evolution of a mixed strategy of cheating and honesty was unlikely in either population. In nature, however, mixed strategies in both populations clearly coexist. In this paper, we demonstrate that when pay-offs are density dependent, a more likely scenario in nature, mixed evolutionarily stable strategies are possible, and we explore the conditions under which alternative strategies of cheating, honesty and retaliation coexist. An important prediction of our model is that the existence of mutually beneficial symbiotic interactions of this sort may be difficult to demonstrate experimentally using simple removal experiments because of density-dependent compensation within the client population. We hypothesize that this may explain why such mutualisms have been previously difficult to detect under field conditions (Cushman & Beattie 1991).

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*Author for correspondence (robert.freckleton@zoology.oxford.ac.uk).

2. CLEANING INTERACTIONS WITH FIXED PAY-OFFS

Our model considers two species: the cleaner, which relies entirely on cleaning as a source of food, and the client. Cleaner and client populations are comprised of individuals that may adopt one of two strategies: cheating or honesty. An honest client allows the cleaner to attend it, whilst a cheating client consumes the cleaner; an honest cleaner removes only parasites from the client, whereas a cheating cleaner removes scales, mucus and tissues.

In our model, species 1 is the client and species 2 is the cleaner, and density is denoted by x. The dynamics of the client population are given by a pair of differential equations, based on the Lotka–Volterra system for two honest mutualistic species (e.g. May 1981), where $\dot{x}$ denotes the differential of x with respect to time:

$$\dot{x}_1^H = r_1 x_1^H (1 - x_1^H - x_1^C + \alpha x_2^H - \beta x_2^C), \tag{2.1}$$

$$\dot{x}_1^C = r_1 x_1^C (1 - x_1^C - x_1^H + \gamma [x_2^H + x_2^C]). \tag{2.2}$$

The superscripts H and C denote the honest and cheating strategies of the two species, respectively. r_1 is the finite rate of increase, or maximal fitness, of the client, whilst α, β and γ determine the fixed per capita pay-offs and penalties of interactions between the species. α is the pay-off to the client conferred by the cleaning activity of the cleaner (e.g. ectoparasite removal); β is the penalty to the client when attended by a cheating cleaner (e.g. in terms of scale and tissue loss); and γ is the pay-off to the client of cheating and eating the cleaner (e.g. a calorific gain).

In accordance with the nature of the client–cleaner symbiosis, we assume: first, that α, β and γ are positive; second, that $\beta > \alpha$, implying that the physiological cost to a client of injuries caused by a dishonest cleaner is greater than the benefit of ectoparasite removal; and third, that $\gamma > \alpha$, implying that the instantaneous benefit to a client from consuming the cleaner is greater than that of being cleaned.

The dynamics of the cleaner population are given by:

$$\dot{x}_2^H = r_2 x_2^H [x_1^H/(x_1^H + x_1^C)](1 - (x_2^H + x_2^C)/(\delta x_1^H) + \varepsilon x_1^H), \tag{2.3}$$

$$\dot{x}_2^C = r_2 x_2^C [x_1^H/(x_1^H + x_1^C)](1 - (x_2^H + x_2^C)/(\delta x_1^H) + \phi x_1^H), \tag{2.4}$$

where r_2 is the finite rate of increase, or maximal fitness, of the cleaner. The term $[x_1^H/(x_1^H + x_1^C)]$ models the effects of cheating by the client on the cleaner population, with cleaner fitness declining in direct proportion to the frequency of cheating by clients. Because cleaners rely entirely on cleaning for food, the abundance of cleaners is limited by the density of honest clients. This density-dependent feedback is achieved through the term $(x_2^H + x_2^C)/(\delta x_1^H)$, where δx_1^H acts as the carrying capacity of cleaners. The pay-off to an honest cleaner of cleaning is given by ε, whilst the pay-off to a cheating cleaner is ϕ. It is assumed that $\phi > \varepsilon$, i.e. that client tissue is more profitable than ectoparasites.

Although formulated differently, the underlying assumption of constant pay-offs and penalties is identical to that of the model of Poulin & Vickery (1995). Our model predicts that a population of cheating clients will always be robust to invasion by honest clients because $\dot{x}_1^C$ will always be greater than $\dot{x}_1^H$. Moreover, because the

client's pay-off from cheating is always greater than the pay-off from honesty, honest clients will always be susceptible to invasion by cheaters. Similarly, from the cleaners' perspective, $\dot{x}_2^C$ is always greater than $\dot{x}_2^H$ under zero net population growth because it is assumed that $\phi > \varepsilon$. Hence, honest cleaners can always be invaded by cheating cleaners, but they cannot invade a population of cheaters. Similar conclusions were reached by Poulin & Vickery (1995).

3. DENSITY-DEPENDENT INTERACTIONS

The assumption of fixed pay-offs is arguably unrealistic. Instead, these are likely to vary with the abundances of cheating and honest cleaners. Specifically, if honest cleaners are rare, then we would expect clients to harbour high ectoparasite loads (e.g. Grutter 1999); the pay-off to a client from a cleaning bout would therefore be high, as would the foraging benefit to the cleaner (e.g. Grutter 1995). Conversely, if honest cleaners are common, then client parasite loads may be lower; the pay-off from a cleaning bout in which relatively few parasites are available for removal would therefore be correspondingly low for both client and cleaner.

In this section we introduce an additional state variable for each client strategy that represents client ectoparasite load. Because cleaners remove ectoparasites (Grutter 1999; Cheney & Côté 2001), the pay-offs to clients from interacting with cleaners are indirectly mediated through ectoparasite load.

Let the mean ectoparasite loads of an honest client and a cheating client be p^H and p^C, respectively. The dynamics of the clients' parasite loads are given by:

$$\dot{p}^H = r_p p^H (1 - p^H - \rho x_2^H), \tag{3.1}$$

$$\dot{p}^C = r_p p^C (1 - p^C), \tag{3.2}$$

where r_p is the rate of increase of ectoparasites from low densities and ρ is the reduction in parasite density per honest cleaner. The ectoparasite load of cheating clients is unaffected by the presence of cleaners (equation (3.2)), so the equilibrium ectoparasite load, $\hat{p}^C$, for cheating clients is always $\hat{p}^C = 1$. For simplicity, ectoparasite loads are modelled relative to this unit load of cheating clients. Thus, the equilibrium load of ectoparasites on honest clients, $\hat{p}^H$, is given by $\hat{p}^H = 1 - \rho \hat{x}_2^H$, in which $\rho \hat{x}_2^H$ is the proportion by which ectoparasite loads are reduced on honest clients relative to cheating ones.

By incorporating parasite loads the dynamics of the client population are now given by:

$$\dot{x}_1^H = r_1 x_1^H (1 - x_1^H - x_1^C - \kappa p^H - \beta x_2^C), \tag{3.3}$$

$$\dot{x}_1^C = r_1 x_1^C (1 - x_1^C - x_1^H - \kappa p^C + \gamma [x_2^H + x_2^C]), \tag{3.4}$$

where the new parameter, κ, is the reduction in client fitness per unit density of ectoparasites. The pay-off to honest clients from being cleaned is now indirect, through the reduction in ectoparasite density with increasing density of honest cleaners.

The equations describing the dynamics of the cleaners are:

$$\dot{x}_2^H = r_2 x_2^H [x_1^H/(x_1^H + x_1^C)](1 - (x_2^H + x_2^C)/(\delta x_1^H) + \varepsilon x_1^H p^H), \tag{3.5}$$

$$\dot{x}_2^C = r_2 x_2^C [x_1^H / (x_1^H + x_1^C)](1 - (x_2^H + x_2^C)/(\delta x_1^H) + \phi x_1^H). \quad (3.6)$$

The pay-off to honest cleaners of cleaning is now given by the constant, ε, multiplied by the ectoparasite load per honest client and the density of honest clients.

(a) Positive equilibria for honesty in cleaner and client populations

We consider first only honest cleaners and clients. Thus, we have:

$$\dot{x}_1^H = r_1 x_1^H (1 - x_1^H - \kappa p^H), \quad (3.7)$$

$$\dot{x}_2^H = r_2 x_2^H (1 - x_2^H / (\delta x_1^H) + \varepsilon x_1^H p^H). \quad (3.8)$$

Setting equations (3.7) and (3.8) equal to zero and solving yields two (nonlinear) simultaneous equations for the densities of the two populations (noting that $\hat{p}^H = 1 - \rho \hat{x}_2^H$; see electronic Appendix A available on The Royal Society's Publications Web site):

$$\hat{x}_1^H = 1 - \kappa + \kappa \rho \hat{x}_2^H, \quad (3.9)$$

$$\hat{x}_2^H = \delta \hat{x}_1^H (1 + \hat{x}_1^H)(1 + \rho \delta (\hat{x}_1^H)^2)^{-1}. \quad (3.10)$$

The expressions for the equilibrium densities involve the solution of cubic equations and are basically uninformative. However, equations (3.9) and (3.10) yield two important results. First, if the density of honest clients is greater than zero then the density of honest cleaners is always greater than zero, because all terms in equation (3.10) are positive. Second, the presence of honest cleaners increases the density of honest clients by an amount $\kappa \rho \hat{x}_2^H$. Thus, densities of honest clients are higher when honest cleaners are present.

(b) Positive equilibria and invasion of cheating strategies

Our model predicts that cheating and honest strategies can coexist at an equilibrium in both populations. First, consider the cleaner population within the full model including both honest and cheating strategies in both species. At equilibrium, equations (3.3) and (3.4) imply:

$$-\kappa \hat{p}^H - \beta \hat{x}_2^C = -\kappa \hat{p}^C + \gamma (\hat{x}_2^H + \hat{x}_2^C). \quad (3.11)$$

Substituting the expression for the equilibrium density of ectoparasites on honest clients and solving yields the equilibrium ratio:

$$\hat{x}_2^C / \hat{x}_2^H = (\kappa \rho - \gamma)/(\beta + \gamma). \quad (3.12)$$

Note that this expression for the ratio of cheating to honest cleaners does not involve any of the parameters that define the dynamics of the cleaner population in equations (3.5) and (3.6). Instead, the probability of cheating by cleaners depends on the relative benefits and costs to clients of cheating, as well as the impact of cleaners on the ectoparasite loads of honest clients. Thus, cheating by cleaners will be favoured if the benefit to clients of being cleaned is high in terms of ectoparasite removal per cleaner (ρ is high), if the cost to clients of harbouring ectoparasites is high (κ is large) or if the penalties to clients of cheating are small (β is low).

These predictions are demonstrated in figure 1, which shows the effect of changing the ratios of κ to γ and γ to β, at two values of ρ. The ratio of κ to γ measures the loss
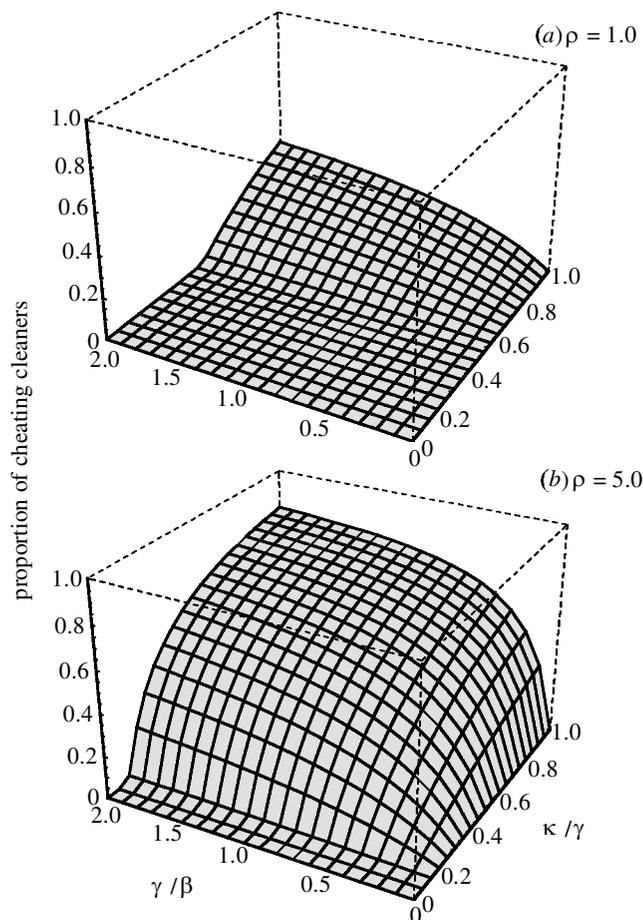
Figure 1. Frequency of cheating within a cleaner population as a function of the ratio of the benefits to clients of cheating (γ) to the costs to clients of meeting cheating cleaners (β), and the benefits to clients from parasite removal by cleaners (κ) relative to the benefits to clients of cheating (γ); for (a) $\rho = 1.0$ and (b) $\rho = 5.0$, where ρ is the reduction in parasite density on honest clients per unit density of honest cleaners.

in client fitness per unit density of ectoparasites, relative to the benefit to the client of cheating, per unit density of cleaners. The ratio of γ to β measures the benefit to clients of cheating, per unit density of cleaners, relative to the cost to clients of meeting a cheating cleaner, per unit density of cheating cleaners. It is clear that increasing either the direct pay-offs to clients of interactions with cleaners, through increasing γ/β or κ/γ, or the indirect pay-offs through increasing ρ, the magnitude of ectoparasite density reduction per cleaner, can greatly increase the probability of cheating by cleaners.

Equation (3.12) further predicts that cheating by cleaners will evolve only when $\rho > \gamma/\kappa$, that is when the magnitude of ectoparasite load reduction per cleaner exceeds the ratio of the benefit to the client of cheating per unit density of cleaner, relative to the cost to the client of harbouring a unit density of parasites. The initial invasion of cheating by cleaners is therefore unrelated to the cost it imposes on clients (i.e. β), although β does influence the ratio of cheaters (equation (3.12)) once cheating has evolved.

Equation (3.12) predicts the ratio of equilibrium densities of cheating to honest cleaners. The actual equilibria are given by (see electronic Appendix A):

$$\hat{x}_2^{\mathrm{H}} = (1 - \phi/\varepsilon)\rho^{-1}, \tag{3.13}$$

$$\hat{x}_2^{\mathrm{C}} = ((\kappa\rho - \gamma)/(\beta + \gamma))(1 - \phi/\varepsilon)\rho^{-1}, \tag{3.14}$$

and the equilibrium density of ectoparasites per honest client is then given by:

$$\hat{p}^{\mathrm{H}} = \phi/\varepsilon. \tag{3.15}$$

This is simply the ratio of the pay-off from cheating by cleaners to the pay-off of honesty, i.e. the density of ectoparasites on clients is entirely dependent on relative pay-offs and penalties to cleaners.

Finding the equilibrium densities of cheating and honest clients is less straightforward. However, analysis of equations (3.3) and (3.4) leads to some simple predictions. Consider a situation in which a population of only honest clients is at equilibrium with a mixed population of cheating and honest cleaners. The equilibrium density of ectoparasites on honest clients is $\hat{p}^{\mathrm{H}} = 1 - \rho\hat{x}_2^{\mathrm{H}}$, and hence, in the vicinity of the equilibrium, equation (3.3) may be written as (noting that $\hat{x}_1^{\mathrm{C}} = 0$):

$$\dot{x}_1^{\mathrm{H}} = r_1\hat{x}_1^{\mathrm{H}}(1 - \hat{x}_1^{\mathrm{H}} - \kappa + \kappa\rho\hat{x}_2^{\mathrm{H}} - \beta\hat{x}_2^{\mathrm{C}}). \tag{3.16}$$

If a rare cheating strategy attempts to invade the client population, then it will have a growth rate given by:

$$\dot{x}_1^{\mathrm{C}} = r_1\hat{x}_1^{\mathrm{C}}(1 - \hat{x}_1^{\mathrm{H}} - \kappa + \gamma[\hat{x}_2^{\mathrm{H}} + \hat{x}_2^{\mathrm{C}}]). \tag{3.17}$$

This is equation (3.4) in which the density of ectoparasites on cheating clients is set to unity ($\hat{p}^{\mathrm{C}} = 1$) because cheating clients are not cleaned. In the initial stages of the invasion, it is assumed that the density of cheating clients is low and hence this density does not contribute significantly to density dependence in equation (3.17). For invasion of cheating clients to occur, equation (3.17) must be greater than zero. At equilibrium, equation (3.16) is equal to zero, so it follows that for the cheating strategy to invade the client population, $\kappa\rho\hat{x}_2^{\mathrm{H}} - \beta\hat{x}_2^{\mathrm{C}} < \gamma[\hat{x}_2^{\mathrm{H}} + \hat{x}_2^{\mathrm{C}}]$, which may be written as:

$$\gamma > \kappa\rho P(\hat{x}_2^{\mathrm{H}}) - \beta P(\hat{x}_2^{\mathrm{C}}), \tag{3.18}$$

where $P()$ is the proportion of each of the cleaner strategies coexisting with honest clients. Thus inequality (3.18) implies that for the cheating strategy to invade the client population, the per capita benefit from cheating and consuming a cleaner must be greater than the net benefit from being cleaned. Although this is not a surprising prediction, because this condition includes the densities of honest and cheating cleaners coexisting with honest clients, the invasion of cheating clients depends on the parameters defining the dynamics of the cleaner population. Thus, unlike the equilibrium density of cheating cleaners (equation (3.12)), the invasion of cheating clients depends on the parameters of both populations.

Finally, consider a population of cheating clients. If all clients cheat then the density of cleaners is reduced to zero. Thus the dynamics of such a population are given by:

$$\dot{x}_1^{\mathrm{C}} = r_1 x_1^{\mathrm{C}}(1 - x_1^{\mathrm{C}} - \kappa). \tag{3.19}$$

If an honest client strategy invades then the dynamics of this strategy are given by:

$$\dot{x}_1^{\mathrm{H}} = r_1 x_1^{\mathrm{H}}(1 - x_1^{\mathrm{C}} - \kappa p^{\mathrm{H}}). \tag{3.20}$$

Although honest cleaners are required for invasion and spread of this honest client strategy, if some honest cleaners do exist, honesty will spread in the client population if $\rho > 0$. More generally, equation (3.20) implies that honesty by clients will be favoured when cheating by clients is common. This is because cheating clients will reduce the densities of cleaners, so that cheating by cleaners becomes unimportant (the losses to cheating cleaners are approximately zero in equations (3.19) and (3.20)). Subsequently, the invasion of honest cleaners will be favoured and cheating by clients selected against; thus, the reduction in ectoparasite loads of honest clients will lead to the spread of honesty.

In summary, we have shown that mixed strategies of cheating and honesty can coexist in both populations. The detailed and short-term dynamics of the system are likely to be complex, however, because they involve a large number of strategies that interact in an essentially nonlinear manner.

(c) *Retaliation by clients*

In many cleaner–client relationships, true cheating by clients is not possible because many clients (especially herbivores) have neither the gape nor the dentition necessary to consume cleaners. However, such clients can nevertheless retaliate against cheating cleaners by attacking them or chasing them off (Bshary & Grutter 2002*a*,*b*).

We modify our model to account for retaliation by clients by replacing x_1^{C}, the density of cheating clients, with x_1^{R}, the density of retaliating clients. The dynamics of the client population are then given by:

$$\dot{x}_1^{\mathrm{H}} = r_1 x_1^{\mathrm{H}}(1 - x_1^{\mathrm{H}} - x_1^{\mathrm{R}} - \kappa p - \beta x_2^{\mathrm{C}}), \tag{3.21}$$

$$\dot{x}_1^{\mathrm{R}} = r_1 x_1^{\mathrm{R}}(1 - x_1^{\mathrm{H}} - x_1^{\mathrm{R}} - \kappa p - \beta' x_2^{\mathrm{C}} - \chi x_2^{\mathrm{C}}). \tag{3.22}$$

In this version of the model the density of parasites (p) is assumed to be the same for both client strategies because both allow cleaning by honest cleaners. Equation (3.21) does not otherwise differ from equation (3.3). In equation (3.22), the new parameter χ is the cost to the client of retaliating against cheating cleaners. We assume that by retaliating, clients are affected less by cheating cleaners than if they do not retaliate (i.e. remained honest). The loss per unit density of cheating cleaners is therefore modified to β', where $\beta' < \beta$.

The dynamics of the system described by equations (3.21) and (3.22) are simple: the client retaliation strategy can invade a population of non-retaliating honest clients when the reduction in losses to cheating cleaners (i.e. $\beta - \beta'$) is greater than the cost to the client of retaliation (χ). The invasion of the retaliation strategy is thus independent of the dynamics of the parasite loads and of the relative levels of cheating and honesty in the cleaner population. If the retaliation strategy can invade, then equation (3.22) will always be greater than equation (3.21), and hence the honest strategy is driven extinct. Thus, populations of clients are predicted to contain either only retaliators or only honest non-retaliators.

When interacting only with retaliating clients, the dynamics of the cleaner population are:

$$\dot{x}_2^{\mathrm{H}} = r_2 x_2^{\mathrm{H}}(1 - (x_2^{\mathrm{H}} + x_2^{\mathrm{C}})/(\delta x_1^{\mathrm{R}}) + \varepsilon x_1^{\mathrm{R}} p), \tag{3.23}$$

$$\dot{x}_2^{\mathrm{C}} = r_2 x_2^{\mathrm{C}}(1 - (x_2^{\mathrm{H}} + x_2^{\mathrm{C}})/(\delta x_1^{\mathrm{R}}) + \phi x_1^{\mathrm{R}} - \theta x_1^{\mathrm{R}}). \tag{3.24}$$

In equation (3.24) the new parameter θ models the reduction in pay-off to cheating cleaners resulting from retaliation by clients.

Consider a population composed solely of honest cleaners. For cheating cleaners to be able to invade, equations (3.23) and (3.24) imply:

$$\phi - \theta > \varepsilon p,$$

where p in this case is the equilibrium density of parasites on clients attended only by honest cleaners. The cheating cleaner strategy will thus invade when the net gain from cheating exceeds the gain from consuming parasites. This will not occur if the penalty to cleaners of cheating (θ) is very high, although not so high that the cost to the client of retaliation (χ) prohibits the invasion of the retaliator strategy. However, if the cleaner population consists solely of cheats, then the density of parasites on clients is unity and the honest strategy can invade if:

$$\phi - \theta < \varepsilon.$$

Thus, mixed strategies of cheating and honesty can coexist in the cleaner population if:

$$\varepsilon > \phi - \theta > \varepsilon p.$$

If the difference between ε and εp is large, i.e. if p is small because honest cleaners are very effective in reducing parasite loads, then there will be a wide scope for mixed strategies to coexist within the cleaner population.

(d) *Perturbations at equilibrium: implications for removal experiments*

Removal experiments in which cleaner numbers are experimentally reduced are a common approach to testing for mutualistic interactions (Cushman & Beattie 1991), but removal frequently does not lead to concomitant decreases in client numbers or fitness (see Côté (2000) for a review). We finally consider responses to perturbations at equilibrium, specifically considering the response of client populations to the removal of cleaners. If clients benefit from being cleaned, then a reduction in cleaner numbers should lead to a concomitant decrease in client density.

Under equilibrium conditions, $\dot{x} = 0$ for both species and both strategies. Client density decreases following cleaner removal when $-\Delta \dot{X}_1 > 0$, where $\dot{X}_1$ is the rate of change in total client density (i.e. $X_1 = x_1^H + x_1^C$) with changing cleaner densities. The rate of change of total client population growth rate with changing cleaner density is given by:

$$\Delta \dot{X}_1 = \left(\frac{x_2^H}{x_2^H + x_2^C}\right)\frac{\partial \dot{X}_1}{\partial x_2^H} + \left(\frac{x_2^C}{x_2^H + x_2^C}\right)\frac{\partial \dot{X}_1}{\partial x_2^C}$$
$$= (x_2^H + x_2^C)^{-1}\left(x_2^H\frac{\partial \dot{X}_1}{\partial x_2^H} + x_2^C\frac{\partial \dot{X}_1}{\partial x_2^C}\right). \quad (3.25)$$

Evaluating this expression at equilibrium (see electronic Appendix A) implies that for a detectable negative impact of cleaner removal on client populations:

$$\gamma < \frac{\hat{x}_1^H(\beta - \hat{x}_2^H \kappa \rho)}{\hat{x}_1^C(\hat{x}_2^H + \hat{x}_2^C)}. \quad (3.26)$$

A decrease in client density following partial removal of cleaners will be recorded only if the ratio of honest to cheating clients is high, if the benefit to clients of cheating is low or if clients' loss to cheating cleaners is much greater than the reductions in ectoparasites by cleaners. If this is not the case, then increases in client populations may be recorded following cleaner removal, even if at an individual level the cleaning interaction is beneficial to the client. This is caused by the combined effects of density dependence and differential changes in the various strategies within the interacting species, which may compensate for the removals. For instance, if many clients cheat then cleaner removals may lead to loss of a food source for clients; if cheating by cleaners is common, then removal of cleaners will lead to a reduction in their negative effects. Thus, removal experiments may frequently fail to reveal the mutualistic nature of interactions. This problem may be partially solved by conducting removals at a large enough scale. However, if cheating by cleaners is common, even large-scale removals of cleaners may not impact negatively on client populations, at least in the short-term.

4. DISCUSSION

Honesty and cheating can coexist in cleaning symbioses among fishes, but only when the benefits of the interaction for honest clients and cleaners are dynamic. As had been noted previously (Poulin & Vickery 1995), we found that when these benefits are fixed, the co-occurrence of honest and cheating strategies is impossible. The inclusion of pay-offs that vary nonlinearly with cleaner density resulted in stable positive equilibria for honesty and cheating within each interacting species. In many client species cheating may not be possible, and our model indicates that the evolution of retaliation against cheating cleaners may be another option for clients. In such cases the evolution of mixed strategies of retaliation and honesty within the cleaner population is similarly possible.

The factors that promote the coexistence of alternative strategies within both populations, namely variable density-dependent pay-offs, are also strongly implicated in generating stability in ecological models of honest mutualistic interactions. Whereas simple models that include only fixed positive effects predict a so-called unstable 'orgy of mutual benefaction' (May 1982), density-dependent feedback (e.g. Goh 1979; Addicott 1981; May 1981) or saturation of positive effects with increasing density can stabilize interactions (e.g. May 1981; Hernandez 1998). In the latter case, for example, the introduction of a third species (such as ectoparasites in a cleaner–client interaction) may be highly stabilizing (Post *et al.* 1981). Therefore, given that variable density-dependent pay-offs are likely to be characteristic of most (stable) mutualisms, it would appear likely that many mutualistic interactions contain the ingredients required for the evolution of mixed strategies of cheating and honesty. Such factors have only just begun to be included in models for cheating in mutualisms (Ferrière *et al.* 2002).

In the context of cleaning symbioses, there is circumstantial evidence that the benefits of honesty in cleaning interactions do indeed vary and depend on cleaner densities. For example, tropical damselfish living close to shore, in areas with low densities of cleaners, harbour more ectoparasites than those living deeper, where cleaners are more numerous (Sikkel *et al.* 2000). Similarly,

clients experimentally or naturally deprived of cleaners in the field suffer significant increases in ectoparasite loads (Grutter 1999; Cheney & Côté 2001). In all cases, client ectoparasite loads, and hence the potential benefits of being cleaned, covary negatively with cleaner numbers. This negative relationship between ectoparasites and cleaner density will also affect the benefits to cleaners of cleaning because cleaner foraging bouts are typically short and intake rates are low on clients with few ectoparasites (Grutter 1996a; Arnal *et al.* 2000).

If the relationship between cleaner and client is mutually beneficial, then reductions in one of the populations should impact negatively on the other. Cleaner removals have already been performed in several field experiments, with the expectation that client numbers should decrease on cleaner-free reefs (Youngbluth 1968; Losey 1972; Gorlick *et al.* 1987; Grutter 1996b, 1997; but see Limbaugh 1961). The fact that all but one of these studies failed to show decreases in client density following partial or total removal of cleaners led to the conclusion that the impact of cleaning on clients may be negligible (Côté 2000). However, our model indicates that the net response of clients to the removal of cleaners depends not only on the positive effects of cleaning, but also on the negative effects of density dependence, which vary with intraspecific population density. If density dependence is strong, then positive effects on individual fitness resulting from interactions between individuals (e.g. from a single cleaning bout) may be measurable, while population-level effects will be undetectable, owing to compensatory density-dependent effects.

The symbiosis we have analysed is one in which cleaners are entirely dependent on clients. This is just one extreme of a range of levels of interpopulation dependency. In many cases, cleaners may clean facultatively, obtaining most of their food from non-client sources (Côté 2000). Although we have not included the possibility of alternative food sources for cleaners in our model, we would expect this to lead to decreased cheating by clients because client cheating would decrease the profitability of cleaning for cleaners and increase the relative benefits of feeding elsewhere. Alternatively, spatially restricted movements of individuals and repeated interactions between the same individuals at specific stations may lead to iterated localized games (Bshary & Grutter 2002a,b). These phenomena are outside the scope of the current analysis, but are likely to play a part in the evolution of mixed honest and cheating strategies.

As noted above, the factors that we have identified as being the key to understanding the evolution of mixed strategies of cleaning and cheating, i.e. density dependence and variable nonlinear pay-offs, are predicted to occur in any persistent mutualism. Thus the analysis presented here is likely to have implications for a range of interactions, particularly obligate relationships, where one population is entirely dependent on the other. Specifically, our model highlights the importance of analysing the pay-offs from interactions in a dynamic context, as well as of separating the individual and population-level consequences of apparently mutualistic behaviours.

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