



Cooperation through interdependence

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Cooperation is fundamental to human societies and widespread among animals, yet explaining how cooperative relationships persist without one party exploiting another remains a challenge. Although it is well established that altruism can be favoured when recipients are relatives or when they reciprocate, it is increasingly being recognized that many behaviours cannot be explained in these terms. Here, I argue that many cases of apparent altruism can be explained by interdependence. I formalize the degree of interdependence by defining an individual's 'stake' in another as the dependence of its fitness on that of the other. This provides a means of valuing others, analogous to Hamilton's valuation of relatives. It also provides a conceptual synthesis of theories of altruism, in which kinship and reciprocity become special cases. Interdependence means that cooperators can benefit as a secondary consequence of helping their recipients. Altruism can then be favoured when its costs are outweighed by the altruist's stake in the recipient's benefits. Whereas the exploitation problem makes reciprocal altruism inherently unstable, cooperation through interdependence can be stable because whatever others do, it is best to cooperate. I discuss the extent to which interdependence can explain examples of cooperation that cannot be explained in terms of kinship and reciprocity.

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Explaining cooperation remains a central focus in the study of animal behaviour. At the core of this problem is how it can ever be in the interests of one individual to help another. Major theoretical advances have shown how this problem can be solved when recipients are kin (Hamilton 1964) or when they reciprocate (Trivers 1971), yet there remain many behaviours that cannot be explained in these terms. In this paper I consider the extent to which cooperation may be explained by individuals being interdependent.

In the following I use the term altruism to refer to where individuals seemingly pay a cost, at least in the short term, to benefit another individual. I use cooperation to refer to where individuals acting together benefit more than they would alone. Note that this is the usage of Roberts (1997) rather than that of Stephens & Anderson (1997). Following common usage when discussing game theory models, I also refer to individuals as cooperating when they follow a 'Cooperate' strategy.

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BACKGROUND

Following Hamilton's (1964) insight, many studies have shown that kinship is a widespread and important predictor of altruistic behaviour (Griffin & West 2003). Nevertheless, there are a number of studies in social insects (Keller 1997), cooperatively breeding birds (Cockburn 1998) and cooperatively breeding mammals (Clutton-Brock et al. 2001a; Clutton-Brock 2002) where relatedness does not explain variance in helping behaviour. For example, in social insects, workers do not always favour more closely related individuals in their colony (Keller 1997). While it can be argued that kin recognition systems are not sufficiently fine-tuned for individuals to distinguish levels of relatedness and allocate help accordingly (Keller 1997), it can also be argued that there may be an adaptive explanation for helping in these instances other than kinship.

The theory of reciprocal altruism (Trivers 1971), although it has enjoyed widespread acceptance, has also been the subject of increasing dissatisfaction (e.g. Clements & Stephens 1995). Attempts to apply the extensive theoretical work on reciprocity (Axelrod & Hamilton 1981) have led empiricists to question its assumptions and predictions (Heinsohn & Packer 1995; Noë et al. 2001). In addition, studies of human behaviour consistently

find that people are more cooperative than economic rationality would predict (Ostrom 1998; Palameta & Brown 1999; Colman 2003; Fehr & Fischbacher 2003). Furthermore, the close relationships among human friends and partners appear to go beyond what is predicted by reciprocity (Tooby & Cosmides 1996; Silk 2003). The failure of current hypotheses to explain human cooperation has led some authors to resort to describing our behaviour as nonadaptive (Gintis 2000) or as adapted to ancestral conditions that no longer apply (Tooby & Cosmides 1996). Current work stresses the potential role of cultural evolution in explaining this tendency to cooperate more than expected from reciprocity theory (Fehr & Fischbacher 2003).

There therefore appears to be a gap between the current state of theories on cooperation and the evidence. To some extent this divide might be bridged by developing models of reciprocal altruism that incorporate more biologically realistic assumptions. Advances in this direction include allowing variable investment (e.g. Roberts & Sherratt 1998), incorporating constraints on resources available for cooperation (Sherratt & Roberts 2001), and considering the social context in which cooperation occurs: if individuals differ in quality and can choose partners then higher levels of altruism are predicted because of 'competitive altruism' (Roberts 1998) or a 'market effect' (Noë et al. 2001).

However, these theoretical developments are still based around reciprocity, or at least some form of trade. As a number of authors have recognized, there is also a need for the more fundamental approach of developing additional and alternative theories (e.g. Connor 1995; Roberts 1998). Any adaptive explanation for altruism at the individual level must explain how individuals profit from altruism in the longer term. Thus, it must explain how the initial costs are offset by some resulting benefit. There has recently been considerable interest in systems where individuals gain indirectly through altruists helping other altruists (Alexander 1987). Such indirect reciprocity has been modelled using image scoring (Nowak & Sigmund 1998) and standing strategies (Leimar & Hammerstein 2001) and has been demonstrated in experiments with human subjects (Wedekind & Milinski 2000).

However, there remains the key question of whether it can ever be in an individual's interests to help others, even if these others never actively return the benefit either directly or indirectly. The main candidate theory is that altruism may be used as a signal, a costly and thereby honest indicator of quality (Zahavi & Zahavi 1997), and that individuals may gain as a consequence of having an altruistic reputation (Roberts 1998). Theoretical work (Lotem et al. 2003) indicates that signalling benefits may offset the costs of altruism, and evidence from turtle hunting behaviour in the Meriam is consistent with this explanation (Smith et al. 2003).

While there is growing evidence for the role of costly signalling in cooperation, some theoreticians have suggested that cooperation could be based on sharing traits that are cost free and essentially arbitrary (Riolo et al. 2001). This suggestion was of interest as it raised the possibility of cooperation without either the need to meet

again or any memory of previous interactions. However, the model turned out to be flawed in that it effectively built in a rule of cooperating with like partners (Roberts & Sherratt 2002). Thus, finding routes to cooperation without reciprocation remains the 'holy grail' of cooperation research.

INTERDEPENDENCE

One possibility is that an altruist might benefit not from the active return of a benefit, but as a secondary consequence. This suggestion is not new (Brown 1983; Connor 1986; Leimar & Connor 2003), and has been developed in the context of group augmentation where helpers at the nest benefit from rearing more group members (Kokko et al. 2001). Nevertheless, it has received remarkably little attention. Here, I argue that such a mechanism deserves further attention and I provide a theoretical underpinning for when we should expect it to be found. The basis for this is interdependence: many apparently altruistic acts have as their beneficiary an individual in whose welfare the altruist has some interest or 'stake'. Where this is true, altruists can be expected to benefit as a secondary consequence of their behaviour. This means that being altruistic could be in one's own long-term best interests, so co-operation could be favoured without reciprocation.

This can be formalized by noting that altruists pay a cost c which benefits a recipient by b . Then, unlike in reciprocal altruism where the recipient actively benefits the original altruist, the altruist gains secondarily as a function of the beneficiary's gain. Denoting as s the altruist's stake in the recipient's benefit, we obtain the expression:

$$sb - c > 0 \quad (1)$$

The conditions in which altruistic acts can be favoured are therefore defined as being when the cost to the altruist c is outweighed by the benefit to the recipient b , devalued by the altruist's stake s in the benefits to the recipient.

What exactly is s ? We can derive this by noting that when an individual B benefits from an act of altruism, its fitness increases from w_B to w'_B , and that as a secondary consequence of this, the altruist A's fitness increases in proportion, the proportionality being given by s . Thus: $w'_A = w_A + s(w'_B - w_B)$. Rearranging, we find:

$$s = \frac{w'_A - w_A}{w'_B - w_B} \quad (2)$$

The stake is therefore a measure of the extent to which changes in the fitness of one individual are reflected in changes in the fitness of another (which can also be expressed as $s = \Delta w_A / \Delta w_B$). This simple formula provides a framework for understanding how it may be in one individual's interests to act in such a way as to increase another's fitness. Essentially, the greater the change in the fitness of A with changes in the fitness of B, the larger the value of s , and the more likely we are to find altruism. Table 1 gives the range of possible values of s , their interpretation, and their implications for the conditions under which altruism can be favoured.

Table 1. Interpretation of values of the stake

Relation between fitness of individuals A and B	s	Conditions where $sb - c > 0$ satisfied	Consequences for altruism
Independent	0	$c < 0$	Never favoured
Positive	$0 < s < 1$	$b/c > 1/s$	Favoured when condition holds
Equivalent	1	$b > c$	Behave as if for self
More dependent on other than on self	> 1	$b/c < 1$	Benefiting partner preferred over benefiting self
Negative	< 0	None	Competition. Spiteful if $b/c > 1/s$ and b and s are both negative

s = the stake of individual A in individual B; b = the benefit to the recipient of altruism; c = the cost to the altruist.

Note that this formulation assumes linear effects of investments on fitnesses. This assumption is made for reasons of simplicity and parsimony. In reality, more complex relations between investments and fitnesses are likely to apply, but it must remain a matter for further empirical work to determine what functions are appropriate and for further theoretical work to determine how these affect the model.

If having a stake in other individuals is the key to altruism, how can the required relations between the fitnesses of different individuals arise? The most familiar reason is kinship, in which case substituting relatedness into the stakeholder equation recovers Hamilton's Rule, whereby altruists benefit as a function of their relatedness r to their beneficiaries, and altruism is performed when $rb - c > 0$. Thus, relatedness can be viewed as an example of a stake, albeit a special case because it is at the genetic rather than individual level that the stake applies.

The second familiar way in which a relation between fitnesses may come about is through reciprocation. That is, the fitness of A will increase with that of B if B has a tendency to reciprocate acts of altruism such that both individuals make a net profit. The stake then becomes equivalent to the probability of reciprocation. Note that while reciprocity theory normally considers only an individual's disposition to cooperate (as reflected in its strategy, such as Tit for Tat; Axelrod & Hamilton 1981) the propensity to reciprocate is also a function of the partner's ability to do so (which might be restricted because of a lack of resources; Sherratt & Roberts 2001). A can therefore increase its probability of benefiting from B, both by behaving in such a way as to encourage a cooperative response and by enhancing B's survival such that it can reciprocate (Eshel & Shaked 2002). Two other special cases are worth noting: first, when reciprocation comes from a beneficiary's offspring (delayed or intergenerational reciprocity; Wiley & Rabenold 1984), the stake also encompasses B's reproduction; and second, when A's benefits come from being observed to be altruistic (indirect reciprocity; Nowak & Sigmund 1998), the stake encompasses all these observers.

However, what is of most interest here is the possibility that even when a recipient is unrelated and does not reciprocate, an altruist may nevertheless receive secondary benefits arising from its behaviour. These benefits could arise as a passive consequence of the recipient's welfare, where welfare is a short-hand for the recipient's survival in such a state as to provide such an effect. For there to be

such secondary benefits, individuals must be interdependent. This condition is met in many social groups: it is a widespread phenomenon that increasing group size brings fitness benefits, most notably in terms of reduced predation risk (Hamilton 1971), for example through increased vigilance (Roberts 1996). This is well illustrated by meerkats, *Suricata suricatta*, in which foraging success, growth, breeding success and survival of all group members increase with group size (Clutton-Brock et al. 2001b). Individual fitness in such groups is therefore linked to the fitnesses of others. Furthermore, individuals within such groups frequently have the opportunity to help to feed or protect the young of others. It is reasonable to suppose that the cost of giving up a food item for a relatively well-fed adult is less than the benefit of this item to a relatively hungry juvenile; similarly, time spent vigilant may be of low cost to an adult (Clutton-Brock et al. 1999) yet have important consequences in reducing a juvenile's predation risk. Another widespread example where individuals are interdependent is in reproductive partnerships. Where rearing offspring depends on contributions from both sexes, the partners' fitnesses will be interdependent and so they can be said to have a stake in each other.

THE STABILITY OF COOPERATION

We have seen that an individual can achieve a net benefit through being altruistic when the secondary benefits received through its interdependence with the beneficiary more than offset the costs (equation 1). However, for the expected case where interdependence is less than complete ($s < 1$), the beneficiary of the altruistic act will increase in fitness more than does the altruist. This means that although individuals can increase their absolute fitness by being altruistic, they suffer a decrease in relative fitness with respect to their recipients. It would therefore seem that those accepting altruism without performing it would do best, and so that interdependence could not lead to altruism becoming established in a population. To investigate this we need to take a game-theoretical approach (Maynard Smith 1982).

In the reciprocal altruism game, cooperators (C) playing each other get a benefit but pay a cost, whereas a defector (D) playing a cooperator gets a benefit without paying the cost (Fig. 1a). Where $b > c$, which will always be the case in reciprocal altruism, the highest payoff, P will be achieved by a defector playing a cooperator

(a)	C	D
C	$b - c$	$-c$
D	b	0

(b)	C	D
C	$b - c + s(b - c)$	$sb - c$
D	$b - sc$	0

(c)	C	D
C	$2sb - c$	$-c + sb$
D	sb	0

Figure 1. Payoff matrices for interactions involving altruism. (a) The reciprocal altruism game; (b) the stakeholder altruism game where one individual pays a cost to benefit another; and (c) the stakeholder altruism game where one individual pays a cost but both share in the benefit. Symbols as in Table 1. The payoffs in (b) and (c) are given by $P'[p_1, p_2] = P[p_1, p_2] + s \times P[p_2, p_1]$, where P' is the payoff for the stakeholder altruism game and p_1 and p_2 are either cooperators (C) or defectors (D).

($P[D, C] > P[C, C] > P[D, D] > P[C, D]$). This fits the familiar Prisoner's Dilemma scenario so, in a single-shot game, defection is always preferred. However, according to the standard conditions for evolutionary stability (Maynard Smith 1982), a population of cooperators could resist invasion by defectors if $P[C, C] > P[D, C]$. This could be satisfied if a cooperator has a stake in its recipient's payoff (Fig. 1b). Here, the payoffs are supplemented with amounts proportional to the payoffs achieved by each individual's partner. From Fig. 1b, we can see that this condition will be satisfied where $b - c + s(b - c) > b - sc$. The condition for evolutionary stability of cooperation therefore simplifies back to equation (1). We can also calculate when cooperation can invade a population of defectors. Denoting p_c as the proportion of cooperators, this will occur when

$$p_c P[C, C] + (1 - p_c) P[C, D] > p_c P[D, C] + (1 - p_c) P[D, D].$$

This also simplifies to equation (1). Thus, when the return an altruist gets through its stake in the recipient's benefits more than compensates for the loss it makes with respect to a defector who does not pay the cost of altruism, cooperation can invade defection and can itself resist invasion. In effect, having a stake in a partner's payoff allows cooperation to 'escape' from the Prisoner's Dilemma. This is because although defectors playing cooperators get a higher payoff than cooperators playing defectors ($P[D, C] > P[C, D]$), the highest payoff of all is

achieved by mutual cooperators ($P[C, C] > P[D, C]$). This means that, unlike in reciprocal altruism, there is no temptation to defect. Exploiting a partner is not worthwhile because a feedback effect ensures that one achieves a higher payoff through benefiting one's partner. Thus, stakeholder altruism can be stable without requiring repeated interactions, whereas reciprocal altruism cannot.

Thus far, I have defined the stake in terms of the interdependence between an altruist and a single recipient. However, the expression for the stake (equation 2) can be generalized such that B represents the beneficiary, which may be either another individual (as above) or the actor itself together with this other individual (Fig. 1c). The latter scenario may be particularly realistic: each individual may face a scenario fitting a one-shot Prisoner's Dilemma (e.g. deciding whether or not to make a costly alarm signal) then, assuming a dilution effect, they may each have a lower predation risk if the other has survived. Whereas reciprocal altruism is essentially a dyadic process, stakeholder altruism is readily generalized to larger groups. Thus, B can represent a group of individuals, either including or excluding the altruist. Where the actor itself is a direct beneficiary of its behaviour, the scenario is better described as a collective action problem rather than one of altruism, but in both there are similar theoretical problems; in the former, the problem of free-riding (not contributing when others do), and in the latter, the problem of cheating (defecting on a cooperator; e.g. Nunn & Lewis 2001). As group size increases, reciprocal altruism declines markedly (Boyd & Richerson 1988). Further work will be required to test whether cooperation through interdependence is any less susceptible to increasing group size.

CONCEPTUAL SYNTHESIS

I now consider how the stakeholder theory relates to other theories of cooperation. As discussed above, kin selection can be seen as a special case of stakeholder altruism in which the stake is genetic. Reciprocity can also be seen as a special case of stakeholder altruism where the stake comes through the probability of reciprocation. The usual focus of reciprocity theory is an individual's disposition to cooperate (its strategy, such as Tit for Tat; Axelrod & Hamilton 1981), but the probability of reciprocation is also a function of an individual's ability to do so. This is the focus of a recent model of 'partnerships', which considers how helping a partner may increase the likelihood of reciprocation through increasing the partner's welfare (Eshel & Shaked 2002). However, the crucial difference between Eshel & Shaked's model and the mechanism proposed here is that in their case return benefits still come through reciprocation, whereas the focus here is on secondary benefits that do not require reciprocal altruism. For example, according to the partnership model, giving a costly alarm call that saved a flockmate's life could be favoured not just because it might increase the propensity of the flockmate to reciprocate, but also because the flockmate is more likely to be around to be able to reciprocate. Compare this with the

stakeholder model where alarm calling could be favoured even without reciprocation if, for example, the continued existence of the flockmate diluted the altruist's risk of predation in the future.

Connor termed pseudoreciprocity the process where one individual performs a costly act to benefit another, such that the altruist will be more likely to benefit as a by-product of the beneficiary's selfish actions in the future (Connor 1986). This process is integral to the stakeholder model, which can be seen as formalizing, extending and generalizing it. Perhaps surprisingly, pseudoreciprocity has received little attention; indeed its usefulness has been questioned (Mesterton-Gibbons & Dugatkin 1997; but see Leimar & Connor 2003). However, this may come down to a terminological debate: other authors consider pseudoreciprocity to be by-product mutualism because the actor behaves in its own long-term best interests (Mesterton-Gibbons & Dugatkin 1997). By-product mutualism is where ordinary selfish behaviour benefits others incidentally (West-Eberhard 1975; Brown 1983). However, there is an important difference in that whereas in by-product mutualism the primary benefit is to oneself and any benefits to others are secondary, in stakeholder altruism the direct benefit is to the other party and benefits to oneself are a secondary consequence. The argument that they are equivalent is analogous to the proposition that reciprocal altruism is simply mutualism because it is in the participants' own interests (Clements & Stephens 1995). However, I consider that just as reciprocal altruism is useful in recognizing the short-term costs and risks of cheating, pseudoreciprocity is useful in recognizing that a behaviour is altruistic in the short term. Mesterton-Gibbons & Dugatkin (1997) consider what they call by-product mutualism and what Connor calls pseudoreciprocity as resulting from the common enemy of an adverse environment. This argument is similar to that of interdependence, but the stakeholder framework adds an explicit feedback mechanism which shows how any given interaction may fit a range of payoff matrices according to the magnitude of the stake.

Group augmentation (Woelfenden 1975) is a term that encompasses the set of processes whereby the fitness advantages of grouping lead to selection for augmenting the group. These have been modelled (Kokko et al. 2001), and it has been found that, given a positive relation between fitness and group size, it could pay a subordinate to help a dominant, thereby increasing the dominant breeders' survival and/or reproductive success. The result can be seen as consistent with the model presented here in that it can pay a subordinate to help when it has a stake in the dominant breeder through the latter's contributions to the group, and thereby to the subordinate's own survival. The passive benefits involved in augmenting a cooperatively breeding group by recruitment of more members can therefore be understood as a special case within the broader class of secondary benefits that may arise from interdependence.

While grouping may be important in leading to interdependence, this does not mean that the mechanism is one of group selection. Stakeholder altruism can be distinguished from trait group selection (Sober & Wilson

1998) because, under the latter, cooperation results from its between-groups advantage outweighing the within-group advantage of a noncooperative individual (e.g. Aviles 2002); in contrast, the stakeholder approach considers that there is a direct advantage to cooperative individuals. Stakeholder altruism therefore does not suffer group selection's inherent problem of destabilization by cheats. Crucially, stakeholder altruism does not share trait group selection's dependence upon differential assortment between groups (whereby cooperators need to interact preferentially with other cooperators), because cooperators do better regardless of their partner's behaviour. Stakeholder altruism does nevertheless provide a link with group selection models since the stake provides a measure of the extent to which individual interest corresponds with that of the group; where there is complete correspondence, selection could be seen as acting on the group. Normally, however, this correspondence will not be complete and so retaining an individual perspective is more informative. Furthermore, different individuals may differ in the stakes they have in the group, so focusing on those individuals rather than at the level of a heterogeneous group is more appropriate.

Finally, we can also compare stakeholder altruism with synergistic selection (Maynard Smith 1989); however, the crucial difference is that synergistic selection depends upon the nonadditive synergistic effect of two cooperators acting together, whereas stakeholder altruists are not dependent upon finding partners sharing their trait.

APPLICATIONS

Cooperation through interdependence is most likely to be found where individual fitness is positively related to group size. There is good evidence that this is the case in a number of cooperatively breeding birds and mammals (Clutton-Brock et al. 2001b). Here, interdependence could help to explain findings that are inconsistent with the theories of kinship and reciprocity. For example, individual helping effort in meerkats does not correlate with relatedness (Clutton-Brock et al. 2001a). Stakeholder altruism provides a plausible and testable alternative. The mechanism of benefiting secondarily can be distinguished from kinship by its prediction that help should be given according to the likelihood of receiving secondary benefits rather than relatedness, e.g. more help should be given to the nondispersing sex. The tendency of female meerkats to feed female pups significantly more than male pups is consistent with this, given that females are the philopatric sex (Brotherton et al. 2001).

Although both reciprocity and stakeholding predict a correlation between investment in altruism by partners (if one shares a stake in another, then the reverse will often be true), we do not expect to find the dynamic Tit for Tat responsiveness predicted for reciprocal relationships. This is because benefiting secondarily is not based upon exchange and so there is no risk of cheating. One case where contingent behaviour was predicted but not found is in pride defence by lionesses, *Panthera leo* (Heinsohn & Packer 1995). If pride defence is framed

not as a Prisoner's Dilemma but as a scenario where lionesses are to varying degrees interdependent, then the behaviour of 'leaders' and 'laggards' is more readily understood.

By no means all groups bring fitness benefits, and even in those that do there is likely to be an optimal level above which fitness declines. Thus, we would expect levels of helping to decline as within-group competition increases. This could be tested, for example in cooperatively breeding mammals under conditions of varying food supply.

Kinship is undoubtedly the most important explanation for cooperation in social insects, but colony foundation by multiple queens is one example where interdependence may be important. Cooperative colony foundation has a number of benefits such as better defence against both conspecifics and predators. Matsuura *et al.* (2002) showed that the survival of a foundress depended on that of her partner. They therefore showed that, despite the inherent reproductive conflict, a larger female could do better by behaving altruistically towards a smaller partner female than by behaving selfishly. Their model bears considerable similarity to that presented here.

There is evidence that the females of some nonhuman primate species are interdependent. Female baboons often form strong bonds, and those females showing greater sociality have more surviving infants (Silk *et al.* 2003). This suggests that relationships have a value, and indeed the Valuable Relationship Hypothesis has been used to explain reconciliation behaviours in macaques (Aureli 1997). The degree of interdependence between individuals has been manipulated by Cords & Thurnheer (1993) who trained longtailed macaques, *Macaca fascicularis*, to perform a cooperative task in which they could get access to food only when their partner fed. The observed increase in reconciliation behaviours was consistent with the notion that the macaques then placed a higher value on their relationship with their partners.

Food-sharing behaviour is widespread in hunter-gatherer societies but is poorly explained by kinship and reciprocity. One potential explanation is costly signalling (Hawkes & Bird 2002; Smith *et al.* 2003), but interdependence provides an additional possibility. Friendship in humans is another candidate example of interdependence. While close cooperative relationships may be characterized by exchange, their dynamics do not seem to fit the contingencies expected in reciprocity (Tooby & Cosmides 1996; Silk 2003). Tooby & Cosmides (1996, pp. 134–135) defined a close or true friend as 'someone who is deeply engaged in your continued survival and in your physical and social welfare (but not necessarily in promoting the propagation of the genes you carry)'. They considered that individuals should help friends without looking for a contingent return: 'instead of being cheated, the primary risk is experiencing a world increasingly devoid of deeply engaged social partners or sufficiently beneficial social partners or both' (Tooby & Cosmides 1996, page 139). Their concept of deep engagement is close to that of interdependence: in both it may be in one's own interests to help another even without a contingent return.

Arguably the most cooperative behaviour of all is that between partners engaged in reproduction, yet theoretical

attention has focused on the conflicts of interest involved. If we consider that one partner may be dependent upon the other for its own reproductive success, then we can see that the stake offers a way to predict when we should expect to find helping behaviours directed at a mate. Examples where males can be seen as investing in females upon which their reproductive success depends include nuptial gifts in insects (Thornhill & Alcock 1983) and courtship feeding in birds (e.g. Helfenstein *et al.* 2003).

While the focus of this paper is on intraspecies social behaviour, the principles are applicable at a range of levels. One potentially important application of the model is to understanding interspecies mutualisms. Despite their widespread occurrence, theory is poorly developed and focuses on the Prisoner's Dilemma framework (Ferriere *et al.* 2002). Because this stresses the risk of cheating, the continued existence of mutualisms is seen as being problematic. However, the feedback effect that is intrinsic to the stakeholder model provides a mechanism for explaining their stability. This is because it sees each mutualistic partner as having a stake in the welfare of the other. If increasing investment in a partner brings increased returns, then the potential issue of exploitation becomes less important (see also Leimar & Connor 2003).

A major issue in evolutionary biology is how higher levels of organization can emerge as a consequence of the coming together of smaller, previously autonomous entities (Maynard Smith & Szathmáry 1995; Michod 1999). As at the level of the formation of societies, at the cellular level there may be a conflict of interest between the advantages of cooperation among smaller entities and the risks of being exploited. These tensions are such that conflict modifiers are considered essential for the viability of the organism (Michod & Roze 2001). The conflicting selection pressures among constituent entities are also key to one of the most controversial topics in evolutionary biology, that of whether selection can ever act at higher levels in the organizational hierarchy (Dugatkin & Reeve 1994). Focusing on the degree of interdependence may help resolve these issues: the closer the interdependence the more highly correlated are selection pressures on component entities, and so the more individual interest correlates with the interest of the whole. Thus, the level of interdependence should predict the relative power of selection operating at different levels in the organizational hierarchy.

There may also be practical lessons that can be learnt from this approach. The perceived conflict between individual and collective optima leads individuals to over-exploit natural resources, to the detriment of all (Ostrom 1998). This is particularly apparent in, for example, the difficulties in achieving compliance with fishing quotas. Currently, the principal theory that offers a solution to such problems is that of reciprocity (e.g. Ridley 1997). However, this requires multiple interactions and is intrinsically unstable. It may be that policy would be better directed at increasing the level of interdependence between individuals and organizations. The term 'stakeholder' is very widely used in environmental management (e.g. Riley *et al.* 2002); the formulation developed here offers a means of quantifying the level of interdependence,

which can then form the basis for policy that ensures parties have stakes in each other. The essence of the tragedy of the commons (Hardin 1968) is that parties can ignore whatever costs they impose on others; where they are stakeholders they cannot do so. With sufficiently strong interdependence, the interaction can move from being a Prisoner's Dilemma to the area of parameter space where cooperation pays best, whatever the other party does. In other words, the solution lies in policy that marries individual interest with collective interest.

DISCUSSION

This paper has highlighted interdependencies as an integral part of social behaviour, and formalized them in terms of the stakes that individuals have in each other, a stake being a quantitative measure of how the fitness of one individual varies with that of another individual or set of individuals. The stake is therefore a measure of commonality, and individuals can be seen as stakeholders in others, placing a value on their welfare, or survival in such a state as to continue to benefit the altruist. Altruists are seen to benefit through a feedback effect, whereby benefiting those in whom one has a stake benefits one's self secondarily. The stakeholder framework represents a potentially important explanation for altruism which, although framed in terms of social behaviour, can be applied to biological entities at a range of levels. It offers a general rule for altruism, whereby the stake increases the probability of benefiting in some way from an investment in altruism.

While it subsumes kinship and reciprocity, it is most important in highlighting the variety of ways of getting a return on an investment in altruism. In particular, it focuses on the class of interactions where there is not a simple trade of benefits, nor is there direct self-interest, but rather benefits come secondarily through benefiting others. The stability of stakeholder altruism means that it need not involve the 'score keeping' that is inherent in reciprocity because of the need to discriminate against cheating. Rather, it involves investing in others in whom one has a stake so as to receive secondary benefits.

This shift in focus provides a theoretical basis for the growing dissatisfaction with reciprocity as an explanation for human friendships, and the resulting concept of 'deep engagement' (Tooby & Cosmides 1996). It also resolves a class of collective action problems that lie at the core of social behaviour (Ostrom 1998): focusing on the stake that individuals have in others shows how contributing, rather than free-riding, can be in one's own long-term best interests. Stakeholder altruism can therefore potentially provide a much sought-after mechanism for achieving cooperation without relatedness, reciprocation, punishment (Boyd & Richerson 1992) or policing (Frank 1995).

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