



Commentary

Cooperating in the face of uncertainty: A consistent framework for understanding the evolution of cooperation

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Abstract

The evolution of cooperative behaviour, whereby individuals enhance the fitness of others at an apparent cost to themselves, represents one of the greatest paradoxes of evolution. Individuals that engage in such cooperative behaviour can, however, be favoured by natural selection if cooperative actions confer higher fitness than alternative actions. To understand the evolution of cooperative behaviour, the direct and indirect genetic benefits that individuals accrue in the present and future must be summed – this can be accomplished without any reference to the colourful vocabulary typically associated with studies of cooperation. When benefits are accrued indirectly through relatives or directly in the future individuals must be able to assess and enhance their probability of accruing those benefits and behave accordingly. We suggest that, in the same way that studies of kin recognition systems improved our understanding of how individuals assess and enhance their probability of accruing indirect benefits, studies of various forms of inheritance and reciprocation recognition systems will improve our understanding of how individuals assess and enhance their probability of accruing future benefits. Recognizing the parallel between studies of indirect fitness and future fitness, at multiple levels of analysis, will move us toward a simpler and more consistent framework for understanding the evolution of cooperative behaviour.

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1. Introduction

Why on Earth do individuals cooperate? Understanding the evolution of cooperation has been a major focus of biology ever since Darwin (1859) pointed out the difficulties that cooperation, exemplified by the sterile castes of social insects, posed for his theory of natural selection. Humans, just like any other animals, are not immune from the problems associated with the evolution of cooperation (Hardin, 1968). Generally, it is expected that natural selection will have favoured those individuals that behaved in ways that maximized their genetic contribution to future generations. If this is true, then selection will have left us with animals that are basically efficient attempting to maximize their benefits while minimizing their costs. In light of this, cooperative behaviour, where individuals enhance the fit-

ness of others at an apparent cost to themselves, seems like an evolutionary paradox.

Evolutionary biologists have made great headway in understanding paradoxical cooperative behaviours by focusing on cooperative breeding systems—breeding systems in which some individuals either delay or completely forego their own reproduction and help to raise the offspring of others (Sherman et al., 1995). Field studies of birds (e.g., Florida scrub jays, *Aphelocoma coerulescens*, Wolfenden and Fitzpatrick, 1984; Seychelle warblers, *Acrocephalus sechellensis*, Komdeur, 1992, 1994a, 1994b), mammals (e.g., meerkats, *Suricata suricatta*, Clutton-Brock et al., 1999, 2001a,b; naked mole rats, *Heterocephalus glaber*, Sherman et al., 1991), and insects (e.g., wasps, Nonacs and Reeve, 1995; Field et al., 1998, 2000; bees, Seeley and Visscher, 1988; ants, Holldobler and Wilson, 1990; termites, Korb and Schmiidinger, 2004) have revealed various forms of mutualism and kin selection that can underlie the evolution of cooperative behaviour in animals (Emlen, 1995; Clutton-Brock, 2002). In parallel, social scientists, anthropologists, and economists have made great strides toward understanding

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cooperation in humans. Studies, using experimental economic games, have revealed various forms of mutualism and reciprocity that can motivate cooperative behaviour in our own species (Wedekind and Milinski, 2000; Fehr and Gächter, 2002; Henrich et al., 2001; Panchanathan and Boyd, 2004; Rockenbach and Milinski, 2006).

There are obvious gains to be made by all by integrating these two fields of research on cooperation, but despite several attempts (e.g., Emlen, 1991; Dugatkin et al., 1992; Pusey and Packer, 1997; Clutton-Brock, 2002, and more recently, Roberts, 2005; Fletcher and Zwick, 2006; Lehmann and Keller, 2006; Nowak, 2006), the two fields have proven stubbornly resistant to integration. One stumbling block to integration is that reciprocity, considered the most common form of cooperation in modern humans (Rockenbach and Milinski, 2006; Nowak, 2006), is apparently rare in the cooperative repertoire of other animals. Bergmüller et al. (2007) argue that another stumbling block to integration of the fields is the confusion over terminology, and they identify four key questions and provide a flow diagram aimed at helping make linkages between the fields. Although we applaud the efforts of Bergmüller et al. (2007), we believe that their approach is unnecessarily convoluted and complex. Here, we provide an alternate, more straightforward, perspective on how the two fields might be linked.

We suggest that understanding the evolution of cooperation and integrating the two fields is simpler than it seems. The first step is to demonstrate that the putative recipient of cooperation does indeed benefit. The second step is to reveal why the donor of cooperation benefits from its behaviour. We argue that the simplest way to do this is to measure the direct benefits, indirect benefits, and future benefits that individuals accrue from cooperative actions and plausible alternative actions. This approach reveals that if benefits are accrued indirectly or in the future then individuals face a fundamentally similar problem: the benefits are accrued with a degree of uncertainty. The final step toward understanding the evolution of cooperation is, therefore, to explain how the donor guarantees the accrual of benefits in the face of uncertainty. We suggest that this is where the two fields

of cooperation research can be better integrated. We consider the various forms of reciprocity to be systems that permit the evolution of cooperative behaviour based on future and uncertain benefits, logically equivalent to kin recognition systems that permit the evolution of cooperative behaviour based on indirect and similarly uncertain benefits.

2. Part I: The recipient's perspective on cooperation

The first step on the road to understanding cooperation is to demonstrate that the putative recipient of cooperation benefits from the donors actions. This seems like it should be trivial but one issue is often taken for granted, or overlooked, in the demonstration of cooperation: fitness is relative. Hence we must first measure a baseline fitness against which to compare the enhancement of fitness caused by cooperation. This is true whether cooperation is being measured in humans or other animals. In the experimental economics literature, which often deals with monetary exchange, one might question whether this has any impact on fitness. In the cooperative breeding literature, all too often the baseline is considered as the fitness of the recipient in the absence of the donor. This is typically assessed by the experimental removal of the donors (Fig. 1a; e.g., Brown et al., 1982; Leonard et al., 1989; Mumme, 1992; Buston, 2004a; Brouwer et al., 2005). For a truly rigorous test, however, the baseline must be defined as the fitness of the recipient in the presence of the donor but in the absence of the cooperative behaviour, and measured by experimental removal of the cooperative behaviour (Fig. 1b). Our tendency to focus on cooperative behaviour that raises the fitness of the recipient above and beyond what it would get in the absence of the donor, rather than what it would get in the absence of the cooperative behaviour, means that we are missing a variety of interesting cooperative behaviours.

The kinds of cooperative behaviours that we potentially are missing can be illustrated with two examples, one from humans and another from fishes. Consider two students (humans) assigned to a group project for which they will be awarded points to be split evenly. The possible outcomes of such group projects

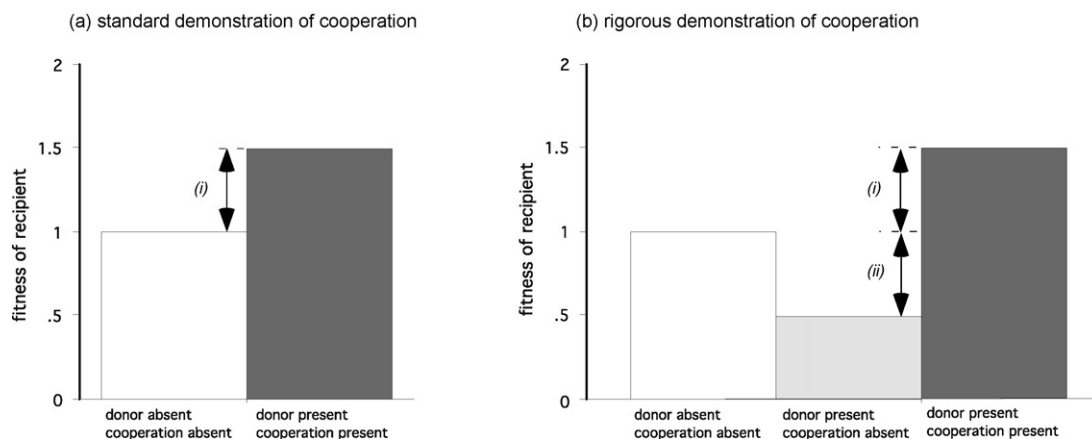


Fig. 1. Cooperative interactions. (a) In general, in the cooperative breeding literature, whether or not cooperation occurs and how much cooperation occurs is assessed by the experimental removal of the donors (black arrow, *i*). (b) In rigorous tests, whether or not cooperation occurs and how much cooperation occurs would be assessed by the experimental removal of the cooperative behaviours (black arrows, *i* and *ii*). Rigorous tests would reveal another large group of cooperative behaviours, e.g., those that donors engage in to offset the costs of their presence (*ii*), in addition to the standard well-documented cooperative behaviours (*i*).

vary wildly (Fig. 1b): the baseline scenario is that students in the group do not get along, exhibit no cooperative behaviours, and actually interrupt each other's active learning so that they achieve a number of points less than that which they would have achieved working independently (light grey); alternatively, students can get along just fine, do not interfere with each other and even express some cooperative behaviours (*i*), and achieve a number of points equal or near equal to that which they would have achieved working independently; finally, the students could get along fantastically, expressing many cooperative behaviours (*i + ii*), and achieving a number of points greater than that which they would have achieved working independently (dark grey). From this simple example, it is apparent that there is a continuum cooperation, involving distinct behaviours: cooperative behaviours are not just helpful, providing benefits above and beyond being alone (Fig. 1a); cooperative behaviours are also peaceful or affiliative, offsetting costs of being together (Fig. 1b).

In several fish taxa, there are breeding systems in which a breeding pair and a few non-breeders share a territory, which bear a striking resemblance to cooperative breeding systems seen in birds, mammals, and social insects (e.g., *Paragobiodon* spp., Lassig, 1976; *Amphiprion* spp., Fricke and Fricke, 1977; *Lamprologine* spp., Taborsky and Limberger, 1981). In two systems studied in detail the presence of non-breeders has no obvious effect on the fitness of the breeders (*Amphiprion percula*, Buston, 2004a; *Paragobiodon xanthosomus*, Wong personal communication), which is commonly taken as evidence that cooperation is not occurring (Fig. 1a, *i* = 0). However, Buston (2003a, 2004a) argued that the presence of non-breeders would be costly and non-breeders would need to engage in cooperative actions to maintain their neutrality (Fig. 1b, *ii* > 0). It is now beyond doubt that non-breeders cooperate: if non-breeders were to arrive in a territory and grow normally then they would become competitors for reproduction and inflict costs on the breeders (Fig. 1b, light grey; Wong et al., 2007); instead, non-breeders regulate their growth to maintain a size at which they are ineffectual competitors and thereby avoid inflicting costs, i.e., provide benefits, to the breeders (Fig. 1b, *ii*; Buston and Cant, 2006; Wong et al., 2007). Interestingly, in the best studied of the cooperative breeding fish systems, non-breeding *Neolamprologus pulcher* also cooperate by regulating their growth (Fig. 1b, *ii*; Heg et al., 2004) but in addition they help with in brood care, territory maintenance and defence against conspecifics (Fig. 1b, *i*; Taborsky, 1985; Balshine et al., 2001; Brouwer et al., 2005). This, once again, highlights that there is a continuum of cooperation involving a wide variety of behaviours that provide benefits and offset costs. What determines the level of cooperation on this continuum is a fast growing area of research (e.g., Kokko et al., 2002; Stiver et al., 2005; Field et al., 2006), and that leads us nicely into the next question: why do individuals engage in cooperative behaviour?

3. Part II: The donor's perspective on cooperation

The second step on the road to understanding cooperation is explaining why the donor of cooperation benefits from its own actions. Although cooperation in nature takes many forms, the

Table 1

Four forms of cooperation, their apparent fitness effect on the phenotype of the donor, and their real fitness effect on the genotype of donor (adapted from Krebs and Davies, 1991)

Cooperation	Apparent fitness effect on donor <i>phenotype</i>	Real fitness effect on donor <i>genotype</i> , relative to alternative actions
Kin Selection	—	+ Because of beneficial effects on close relatives
Mutualism	+ When benefits are immediate — When benefits are delayed	+ Because of beneficial effects on donor
Reciprocity	+ When benefits are immediate — When benefits are delayed	+ Because of beneficial effects of exchange
Manipulation	—	+ Because of costs of escaping cooperation

evolution of cooperative behaviour has, classically, been understood in the context of four hypotheses: kin selection; mutualism; reciprocity; manipulation (Table 1; Krebs and Davies, 1991). All of these hypotheses reveal that, although an individual's phenotype appears to be behaving altruistically, the individual is ultimately behaving in a manner that serves the best interests of its selfish genes (Table 1; Dawkins, 1982). The key to understanding the evolution of cooperative behaviour, lies in recognizing that an action will be favoured by natural selection not simply if it confers the highest fitness, but rather if it confers higher fitness than alternative actions available to the individual given its social and ecological context (Table 1; Reeve and Sherman, 1993).

The classical explanation for cooperation, which has received the most attention amongst evolutionary biologists because it provides the solution to Darwin's puzzle, is kin selection, where natural selection favours individuals that behave cooperatively because they accrue indirect genetic benefits through their relatives (Hamilton, 1964; Brown, 1980; Griffin and West, 2003). The other explanations for cooperation are mutualism, reciprocity, and manipulation, where natural selection favours individuals that behave cooperatively because they accrue direct genetic benefits (Clutton-Brock, 2002). The benefits of mutualism and reciprocity can be accrued immediately (in the present) or with a delay (in the future), e.g., two individuals may work together to defend a breeding territory, one may breed immediately while the other delays reproduction but stands to inherit the territory and breed in the future. Delayed mutualisms and delayed reciprocity often go hand in hand with the threat of punishment or some form of manipulation, by which the recipient of cooperation forces, dupes, or coerces the donor into behaving cooperatively (Clutton-Brock and Parker, 1995; Rockenbach and Milinski, 2006; Wong et al., 2007). We consider by-product mutualism and pseudo-reciprocity, sometimes put forward as causes of cooperation, to be empty concepts, for two reasons: (1) because all benefits, regardless of their source or the intent with which they are accrued, contribute to selection for cooperative behaviour and (2) there are no testable predictions that

enable us to discriminate by-product mutualism from mutualism or pseudo-reciprocity from reciprocity.

In recent years, in the cooperative breeding literature, there has been a shift from focusing on indirect benefits of cooperative behaviour, to focusing on direct benefits and future benefits of the behaviour (Clutton-Brock, 2002). In studies of human cooperation, kin selection has been largely overlooked in favour of reciprocity (especially indirect reciprocity) as the cause of cooperative behaviour (Rockenbach and Milinski, 2006; Nowak, 2006), but recent research suggests that kin selection is likely to have played a central role in shaping cognitive abilities and selecting for the evolution of cooperative behaviour in humans (Bowles, 2006). Moreover, theory tells us that direct, indirect, and future benefits are all important (Box 1) and empirical studies demonstrate that each source of benefits can operate in isolation (e.g., direct, Packer et al., 1991; indirect, Emlen and Wrege, 1989; future, Buston, 2004b). Most importantly, in many cases individuals likely accrue benefits from multiple sources, directly and indirectly, in the present and the future, and thus studying all sources of potential benefits is necessary (e.g., Wilkinson, 1984; Balshine-Earn et al., 1998; Clutton-Brock et al., 2001a; Field et al., 2006). Not only is it necessary, but also it will enhance our understanding because it will enable us to measure the contribution of one source while controlling (statistically or experimentally) for the effect of other sources. While the classical framework (Krebs and Davies, 1991) has served us well, we consider that the evolution of cooperative behaviour is most simply understood by focusing on when and where the benefits of cooperation are accrued: directly or indirectly, in the present or in the future (Box 1).

Here, we have shown that the evolution of cooperative behaviour can be understood by referring solely to the logic and mathematics (Box 1), without reference to any of the colourful vocabulary that is typically associated with studies of cooperation—vocabulary that we consider a distraction and only serves to confuse (e.g., Bergmüller et al., 2007). We advocate the framework laid out in Box 1, rather than the classical framework summarized in Table 1, because it explicitly recognizes that (i) benefits can be accrued from multiple sources and (ii) the benefits of cooperative actions are assessed relative to alternative actions. Additionally, we think this framework (Box 1) helps to draw out a fundamental similarity that exists between cooperative behaviour favoured by kin selection and cooperative behaviour favoured by delayed mutualism or delayed reciprocity (Table 1; see also Roberts, 2005 and Nowak, 2006). Specifically, individuals engaged in cooperative behaviour where the benefits are not immediately apparent, because the benefits are accrued through kin or in the future, must be able to assess the probability with which they will accrue those benefits (r or f , Box 1). This logical parallel between indirect fitness and future fitness brings us to our next topic, and how we think different fields of research on cooperation can be most naturally integrated.

4. Part III: Cooperating in the face of uncertainty

For natural selection to favour the evolution of cooperative behaviour by indirect benefits or future benefits the individuals

Box 1. Understanding the evolution of cooperative behaviour relies on identifying the costs and benefits of cooperative and alternative actions, for the donor and its relatives, now and in the future

Direct benefits

Whether or not cooperation will be favoured by selection can be determined using a simple inequality. In particular, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j > 0 \quad (1)$$

where X_i (or X_j) is the personal reproductive output associated with the i th (or j th) action. Inequality 1 can be used to understand why cooperation evolves as a result of immediate mutualism, immediate reciprocity, or manipulation.

Indirect benefits

Additionally, if $X_i - X_j < 0$, cooperation can still be favoured because of its beneficial effects on kin. The behaviour favoured by selection can be determined by the use of Hamilton's rule (Hamilton, 1964). In particular, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + r(Y_i - Y_j) > 0 \quad (2)$$

where Y_i (or Y_j) is the other individual's reproductive output, and r is the probability that the two individuals share a copy of a particular gene identical by descent (the coefficient of relatedness). Inequality 2 can be used to understand why cooperation evolves as a result of kin selection.

Future benefits

Alternatively, if $X_i - X_j < 0$, cooperation can still be favoured because of its beneficial effects in the future. The behaviour favoured by selection can be determined using inequalities that consider the future (e.g., Kokko and Johnstone, 1999). Most simply, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + f(Z_i - Z_j) > 0$$

where Z_i (or Z_j) is the personal reproductive output associated with the i th (or j th) action in the future, and f is the probability that those benefits will be realized. Inequality 3 can be used to understand why cooperation evolves as a result of delayed mutualism or delayed reciprocity.

All benefits

Of course, hypotheses for the evolution of cooperation are not mutually exclusive; cooperation can be favoured because of its present direct benefits, present indirect benefits, and future direct benefits. (We consider that the effect of future indirect benefits may be weak because it involves a combination of two probabilities r and f .) Thus, generally, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + r(Y_i - Y_j) + f(Z_i - Z_j) > 0 \quad (4)$$

We envisage that this general inequality for the evolution of cooperative behaviour will enable us to make sense of all cases of cooperation in nature.

must be able to assess and/or enhance the probability of accruing those benefits and behave accordingly. It is widely appreciated that for cooperative behaviour to be caused by indirect benefits (kin selection; Box 1, inequality 2) organisms must have the ability to recognize kin (Hamilton, 1964; Sherman et al., 1997). This does not mean that the donor has to know the genotype of the recipient, but rather the donor must have some simple rule, or kin recognition system, that enables it to discriminate kin from non-kin with a reasonable degree of certainty most of the time, e.g. a simple rule that says chicks in your nest are likely to be your offspring and you should feed and protect them accordingly (Sherman et al., 1997). What is not widely appreciated, however, is that for cooperative behaviour to select for via future benefits (delayed mutualism or delayed reciprocity; Box 1, inequality 3) organisms must have equivalent simple rules, or recognition systems to assess the likelihood of accruing future benefits. We suggest that such future recognition systems can be understood using the same evolutionary framework that is used to understand kin recognition systems.

Natural selection would, obviously, favour donors whose recognition systems permitted them to identify the probability that a recipient shares a copy of an allele identical by common descent (r), or the probability that benefits will be realized in the future (f), without error and dispense cooperative behaviour accordingly (Box 1, inequality 4). In reality, however, donors will not be able to perfectly discriminate between more desirable and less desirable recipients of their cooperative behaviour, because such recipients likely will exhibit overlapping phenotypes. This means that donors must trade-off acceptance errors (behaving cooperatively toward undesirable recipients) against rejection errors (not behaving cooperatively toward desirable recipients) to achieve the optimal behaviour (Fig. 2; Reeve, 1989). Natural selection can shape the recognition system to achieve the optimal balance between acceptance errors and rejection errors, by acting on (i) the cues that donors use to recognize recipients, (ii) the algorithm that donors use to clas-

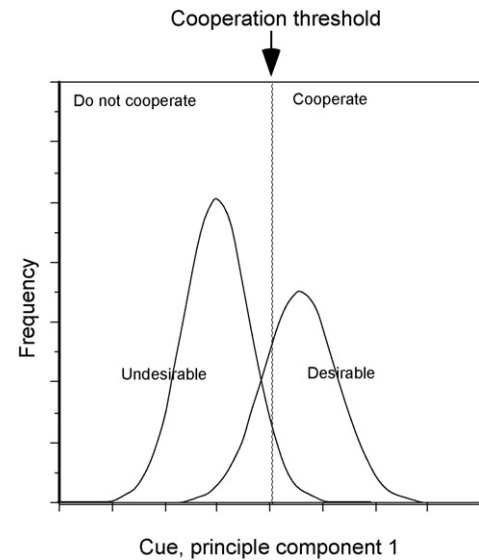


Fig. 2. Recognition systems. The figure illustrates hypothetical frequency distributions of a cue (or first principle component of multiple cues) for desirable and undesirable recipients of a donor's cooperative behaviour. Almost always, the cue distributions of desirable and undesirable recipients will overlap, and the donor will have to trade-off some rejection errors and some acceptance errors. The donor's optimal cooperation threshold, which evolves in response to selection, will depend on the relative rates of interaction with desirable and undesirable recipients and the fitness consequences of appropriate and inappropriate responses. In the case of kin recognition systems, the cues would be associated with the probability of sharing alleles identical by descent. In the case of inheritance recognition systems, the cues would be associated with the probability of inheritance. In the case of reciprocation recognition systems, the cues would be associated with the probability of reciprocation (adapted from Reeve, 1989).

sify recipients, or (iii) the donor's phenotypic response to the classification of a recipient (Sherman et al., 1997). The key to understanding the evolution of recognition systems is to realize that alleles facilitating recognition spread, neither because they allow perfect discrimination, nor because they see copies of themselves being produced by kin or in the future, but rather because they enable an individual to act on a statistical association between cues and the probability of accruing benefits.

4.1. Kin recognition systems

For natural selection to favour individuals that behave cooperatively because they expect to gain indirect genetic benefits (e.g., Hamilton, 1964; Sherman, 1977, 1981; Emlen and Wrege, 1988, 1989), individuals must have some means of assessing and/or enhancing the probability that the individuals they cooperate with share genes identical by common descent—kin recognition systems. Kin recognition cues can be genetic (Grosberg and Quinn, 1986; Holmes, 1986) or environmental in origin (Gamboa et al., 1986; Breed et al., 1995), and these phenotypic cues can be complemented by spatial (Hoogland and Sherman, 1976) and temporal cues (Mumme et al., 1983; Koenig et al., 1995). Kin recognition templates can be genetically encoded (e.g., parent birds accepting young inside their nest but not outside, Hoogland and Sherman, 1976), or learned from environmental cues (Pfennig et al., 1983), parents (Sharp et al., 2005),

or nest mates (Holmes and Sherman, 1982), and self-inspection (Hauber and Sherman, 2001). Finally, actions that are a response to kinship can be binary (Hoogland and Sherman, 1976) or continuous (Neff and Gross, 2001), and vary across space and time (Gamboa et al., 1991). Thirty years of work on kin recognition has given us a clear understanding of the mechanisms that permit the evolution of cooperative behaviour based on indirect genetic benefits (reviewed by Sherman et al., 1997).

4.2. *Future recognition systems 1: inheritance recognition systems*

For natural selection to favour individuals that behave cooperatively because they expect to inherit resources and breed in the future (e.g., Wolfenden and Fitzpatrick, 1984; Creel and Waser, 1994; Field et al., 1999, 2006; Buston, 2003a, 2004b), individuals must have some means of assessing and/or enhancing the probability of receiving that inheritance—inheritance recognition systems. Such systems obviously would not permit individuals to see what is going to happen in the future, but they would permit individuals to act on a statistical association between cues and the probability of inheritance. The best understood cue to the probability of inheritance is the length of social queues: all other things being equal, the probability of inheriting a breeding position is lower at the back of long queues. Wasps and cichlids respond to this cue and exhibit preference for shorter queues (Field et al., 1999; Stiver et al., 2004), but clownfish do not presumably because of the costs of searching among queues (Parker, 1983; Elliott et al., 1995; Buston, 2003b). It's also plausible that individuals will cue in on relative health or likelihood of predation, since the probability of inheritance also depends on relative mortality rates (2004b; Mesterton-Gibbons et al., 2006), though to date there is no evidence for this. Inheritance recognition templates may be genetic because there is little spatio-temporal variability in the characteristics of desirable queues—shorter is generally better. Finally, we know that animals adjust their level of cooperation in response to the probability of inheritance: wasps and cichlids reduce their level of helpful cooperation toward the front of the queue, thereby increasing their probability of inheritance by reducing their work associated mortality rate (Stiver et al., 2005; Field et al., 2006); conversely, clownfish and coral gobies maintain their level of peaceful cooperation throughout queues, thereby maximizing their chance of inheritance by reducing their eviction associated mortality rate (Buston, 2004b; Buston and Cant, 2006; Wong et al., 2007). Clearly, the study of inheritance recognition systems is in its infancy and we have a long way to go before we understand production, perception, and action components of inheritance recognition systems as well as we understand the components of kin recognition systems.

4.3. *Future recognition systems 2: reciprocity recognition systems*

For natural selection to favour individuals that behave cooperatively because they expect to have their cooperation reciprocated in the future (e.g., Trivers, 1971; Packer, 1977;

Wilkinson, 1984; Wedekind and Milinski, 2000; Bshary and Grutter, 2006; Rockenbach and Milinski, 2006; Schino, 2006) individuals must have some means of assessing and/or enhancing the probability that their cooperation will be reciprocated, either directly or indirectly—reciprocity recognition systems. Such systems, once again, would not permit individuals to see what is going to happen in the future, but they would permit individuals to act on a statistical association between cues and the probability of reciprocity. Cues to the probability of reciprocity might involve a combination of individual recognition cues (Dale et al., 2001; Tibbets, 2002) and cues as to the behaviour of individuals. The latter cues might be based on observation of reciprocity or experience of reciprocity (Trivers, 1971; Fehr and Fischbacher, 2003), based on status, reputation and gossip (Nowak and Sigmund, 1998; Rockenbach and Milinski, 2006), or based on assessment of an individual's ability to reciprocate (Sherratt and Roberts, 2001). Reciprocity recognition cues might also be contextual, for example donors might cooperate only in places where they are likely to meet the recipient again (Wilkinson, 1984) or in situations when observers are present (Wedekind and Milinski, 2000). Reciprocity recognition templates may have a genetic component (e.g., if probability of reciprocity were consistently correlated with recipient testosterone levels, then donors could cue in on signals associated with testosterone levels in recipients), but they are also likely to be regularly updated based on learning and experience. As humans we know that we update our opinions of how cooperative individuals are (our reciprocity recognition template) in response to their behaviour toward us and toward others (Fehr and Fischbacher, 2003), and it seems reasonable to suggest that animals that have long-term social relationships do the same. Finally, it seems likely that individuals adjust their level of cooperation in response to the probability of reciprocity: individuals may begin with low levels of investment until trust is built, and cut investment or engage in punishment when there is failure to reciprocate (Connor, 1995; Roberts and Sherratt, 1998; Wedekind and Milinski, 2000; Rockenbach and Milinski, 2006). While there is a long way to go before we understand production, perception, and action components of reciprocity recognition systems as well as we understand those components of kin recognition systems, by using a consistent evolutionary framework there is hope of coming to a clearer understanding of the issue.

5. Discussion

In summary, understanding the evolution of cooperative behaviour, whereby individuals enhance the fitness of others at an apparent cost to themselves, has been one of the greatest challenges of biology and the social sciences (Darwin, 1859; Hardin, 1968). It is becoming clearer day-by-day that the cooperative behaviour of humans and other animals can be understood simply, by applying the rigorous logic of natural selection theory (Dawkins, 1982; Reeve and Sherman, 1993) and seeking out the simplest mathematical expression of the ideas (Box 1; Roberts, 2005; Nowak, 2006). These simple mathematical rules reveal that when cooperation is based on indirect genetic bene-

fits (kin selection) or future genetic benefits (delayed mutualism or delayed reciprocity) individuals face a fundamentally similar problem: they must deal with uncertainty. The evolution of cooperative behaviour based on such benefits requires that individuals assess and/or enhance the probability of accruing those benefits. How organisms manage such assessment can be understood using the unified evolutionary framework of recognition systems (Fig. 2; Reeve, 1989; Sherman et al., 1997). Integrating these concepts will move us toward a consistent framework for understanding the evolution of cooperative behaviour.

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