Review

Cooperation beyond the dyad: on simple models and a complex society

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Players in Axelrod and Hamilton's model of cooperation were not only in a Prisoner's Dilemma, but by definition, they were also trapped in a dyad. But animals are rarely so restricted and even the option to interact with third parties allows individuals to escape from the Prisoner's Dilemma into a much more interesting and varied world of cooperation, from the apparently rare 'parcelling' to the widespread phenomenon of market effects. Our understanding of by-product mutualism, pseudo-reciprocity and the snowdrift game is also enriched by thinking 'beyond the dyad'. The concepts of by-product mutualism and pseudo-reciprocity force us to think again about our basic definitions of cooperative behaviour (behaviour by a single individual) and cooperation (the outcome of an interaction between two or more individuals). Reciprocity is surprisingly rare outside of humans, even among large-brained 'intelligent' birds and mammals. Are humans unique in having extensive cooperative interactions among non-kin and an integrated cognitive system for mediating reciprocity? Perhaps, but our best chance for finding a similar phenomenon may be in delphinids, which also live in large societies with extensive cooperative interactions among non-relatives. A system of nested male alliances in bottlenose dolphins illustrates the potential and difficulties of finding a complex system of cooperation close to our own.

Keywords: cooperation; by-product mutualism; pseudo-reciprocity; reciprocity; alliances

1. INTRODUCTION

The evolution of our understanding of cooperation in the biological world over the past few decades would make for an interesting study on the psychology of scientists and the sociology of a scientific community. A PhD student in the social sciences would begin her investigation perhaps, in the period after the Lack–Hamilton–Williams paradigm shift from a levels of selection muddle to a clear appreciation of the importance of individual selection for shaping adaptation. During that time, while the importance of Hamilton's (1964) kin selection theory was slowly permeating through the community of evolutionary biologists, the problem of helping behaviour directed at non-relatives was emerging as an important outstanding problem. Trivers' (1971) landmark paper on reciprocity held enormous appeal because of the obvious importance of reciprocity in human relationships and the possibility that reciprocity would provide an explanation for a range of interactions among non-humans. Although Trivers (1971) thought that reciprocity would be found in many species, his brilliant discussion of human reciprocity, including the problem of subtle cheating and the role of our psychological system in mediating reciprocal interactions, implied to many readers that reciprocity requires considerable cognitive abilities. The idea

that reciprocity might be limited to animals with significant cognitive abilities was shattered with the publication of Axelrod & Hamilton's (1981) enormously influential publication on the evolution of cooperation. The champion of their Iterated Prisoner's Dilemma model, the tit-for-tat strategy, was exceedingly simple and potentially could be employed in a huge range of interactions, 'not only might two bacteria or monkeys play tit-for-tat, the model could also apply to the interactions between a colony of bacteria and, say, a primate serving as a host' (Axelrod & Hamilton 1981, p. 1392).

Axelrod & Hamilton's (1981) paper set the theoretical community on fire. Top journals such as *Nature* and *The Journal of Theoretical Biology* were frequent hosts to exciting new models of cooperation, reminding one of a runaway selection process (see also the review by Hammerstein 2003). Axelrod & Hamilton's (1981) model begat a number of 'sexy sons' that were interesting exercises in abstraction but had tenuous links to natural phenomena. In contrast, simpler theories of cooperative interactions among non-relatives, such as by-product mutualism (West-Eberhard 1975) and pseudo-reciprocity (Connor 1986), were much less interesting to theorists. However, not all notable theorists were in lock-step on this issue and I suspect that two of the prominent dissidents among their ranks, Leimar & Hammerstein (2010), have played a key role in the recent interest in the simpler explanations (Clutton-Brock 2009).

Thinking 'beyond the dyad' has played an important role in allowing us to escape the confines of the

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One contribution of 14 to a Theme Issue 'Cooperation and deception: from evolution to mechanisms'.

Prisoner's Dilemma. The emergence of theory and empirical work on market effects in animal interactions (Noë & Hammerstein 1995) was an extremely important development. Others built on Trivers' (1971) insightful discussion of multi-party interactions in humans to further explore the complexity of human reciprocity including audience effects, indirect reciprocity (Alexander 1989; Nowak & Sigmund 2005; see also Earley 2010) and the role of policing in human social interactions (e.g. Boyd *et al.* 2003). However, the topics of market effects and human cooperation are simply too large to be evaluated in any depth here. Instead, I touch on market effects briefly and focus more on several evolutionary models of cooperation that may occur not only between individuals but also 'beyond the dyad', including a possible case of reciprocity, by-product mutualism, the snowdrift game and pseudo-reciprocity.

Why has the search for reciprocity among non-humans not been more successful? To understand this we may have to return to the pre-Axelrod and Hamilton idea of some kind of cognitive limitation on the practice of reciprocity. Hauser *et al.* (2009) have argued that a cognitive adaptation that integrates a range of specific cognitive mechanisms required for score-keeping reciprocity was uniquely favoured in humans because of our unusual socio-ecology. For additional views on this topic, see Brosnan *et al.* (2010) and Melis & Semmann (2010). It is important to note that Hauser *et al.* may be correct about a link in humans between an integrated cognitive system and our socio-ecology, even if it is demonstrated that trained apes can engage in simple reciprocity (de Waal & Suchak 2010). Thus we can ask if the elements of human socio-ecology that favoured the cognitive adaptations for reciprocity are really unique. The closest parallel to the particular human socio-ecological characteristics discussed by Hauser *et al.* may be in members of the dolphin family, Delphinidae. The most complex social relationships described to date for any delphinid are found in Shark Bay, Western Australia, where male bottlenose dolphins exhibit a system of nested alliances similar to that found in humans. The males are clearly cooperating, but it is worth considering how the different evolutionary models of cooperation, including reciprocity, may contribute to our understanding of male dolphin alliance behaviour.

From a cognitive perspective, cooperation is only one of a set of problems facing male dolphins. By considering dolphin cooperation in the broader context of social complexity and cognition, it becomes clear that dolphin societies may offer the best hope for finding a human-like system of reciprocity in a non-human species.

2. EVOLUTIONARY MODELS OF COOPERATION

(a) *By-product mutualism*

By-product benefits are derived from self-serving behaviours (Connor 1986; Brown 1987). An individual who is the first to detect a stalking predator will flee to save its life, but that act also informs others in the area of the impending danger. The exchange of

by-product benefits constitutes a by-product mutualism (West-Eberhard 1975; Connor 1995a). This pervasive category of cooperation encompasses an astonishing range of inter- and intraspecific phenomena, including group formation based on the dilution effect, Mullerian mimicry, cooperation between unrelated stranger figs, many examples of cooperative hunting, etc. (Connor 1995a). In many cases, individuals may enhance the by-product benefits they receive by coordinating their behaviour with others, as in fish driving by cormorants (Bartholomew 1942) or killer whales that cooperate to create waves that wash seals off ice flows (Smith *et al.* 1981; Visser *et al.* 2008).

(i) *The definition of cooperation, cooperative behaviour and by-product mutualism*

Sachs *et al.* (2004) and Bergmüller *et al.* (2007) defined cooperative behaviour as 'an act performed by one individual that increases the fitness of another'. West *et al.* (2007) criticized this definition because it 'may be overly inclusive. For example, when an elephant produces dung, this is beneficial to the elephant (emptying waste), but also beneficial to a dung beetle that comes along and uses that dung. It does not seem useful to term behaviours such as this, which provide a one-way by-product benefit, as cooperation'.

West *et al.*'s (2007, p. 419) solution to this problem is to define cooperation (a term they use to describe the behaviour of an individual) as behaviour, 'which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient'. They later qualify this definition, 'we do not wish to imply that the behaviour is selected for purely because of its beneficial effect on the recipient, just that it has at least partially done so'.

While West *et al.*'s (2007) definition of cooperation (or cooperative behaviour) covers investment in others (pseudo-reciprocity and reciprocity), it does not handle by-product mutualisms as well, where actors behave in ways to increase the receipt of by-product benefits from others, but in doing so confer by-product benefits as well. Consider the example they use to illustrate their point, 'suppose that two bacterial species (A and B) are interacting, and that each feeds upon a waste product of the other. This would be a mutually beneficial behaviour (+,+) but we would not classify it as cooperation' (p. 418). For the interaction to merit being called cooperation, West *et al.* (2007) would require that one species of bacteria invest in the other (e.g. by making more waste product). However, there is no such investment in by-product mutualisms, which include some of the most spectacular cases of cooperation found in nature (Connor 1995a).

Consider a simple scenario where fish-eating birds pursue schooling fish and that, initially, the population of birds consists of solitary feeders. If two birds pursuing the same fish school just happen to move close to each other they will each obtain by-product benefits (fish fleeing one bird may swim into the path of the other). This is not cooperation because the benefits derive from an accidental association rather than

selected behaviour. Imagine a mutation in this population of solitary foragers that causes individuals to join others when feeding. This selected 'joining' behaviour would be cooperative because both individuals benefit; but the benefit to the recipient is not the reason selection favours the behaviour. Likewise, members of one species of bacteria (e.g. A) might have an adaptation to join members of species B because the cost of joining is outweighed by the by-product benefits obtained from species B. This would be a by-product mutualism according to Connor (1995a, p. 433), 'if one of the parties in a mutually beneficial interaction exhibits some trait that appears to have been modified for obtaining benefits from the other'. So the interaction between A and B is mutualism but is it cooperation? It is not problematic to define an interaction as a mutualism but not cooperation, as mutualism does not have to be maintained by cooperative behaviours or traits in both parties (one party in a mutualism may 'extract' benefits; see Connor 1995a).

Thus, we can define cooperative behaviour as that *which provides a benefit to another individual (recipient), and which is selected for because the actor's behaviour yields a direct benefit from the receiver*. The benefits returning to the actor include investment and by-product benefits (Connor 2007). This definition is not vulnerable to the elephant-dung problem and it does not require that the recipient benefit for selection to favour the behaviour by the actor. Thus, if only bacteria A has an adaptation to approach B, then we would say that bacteria A behaves cooperatively to produce a by-product mutualism.

Sometimes, what appears to be cooperative behaviour, for example, one monkey handing a piece of food to another, may be an example of *extracted* benefits (Connor 2007). A dominant monkey could coerce food from a subordinate or a subordinate could harass a dominant until the dominant surrendered some food. In both cases the benefit of behaving cooperatively is to reduce costs imposed by the recipient. To include extracted benefits, we can modify our definition of cooperative behaviour to that *which provides a benefit to another individual (recipient), and which is selected for because the actor's behaviour yields a direct benefit from the receiver, or reduces costs imposed by, the receiver*.

It is useful to maintain a distinction between the actions of an individual in an interaction (cooperative behaviour, or we can say an individual behaves 'cooperatively') versus the outcome of the interaction where both parties benefit from the interaction (cooperation).

Many, I suspect, would like to reserve the term cooperation to the outcome of an interaction where both parties behave cooperatively. Thus, the examples of extracted cooperative behaviour are not examples of cooperation; a dominant monkey that gives up some food to a harassing subordinate does not benefit from the interaction. Both parties behave cooperatively in reciprocity and in by-product mutualisms where both parties (e.g. bacteria A and B) had an adaptation to approach each other to receive by-product benefits.

However, both parties do not behave cooperatively in by-product mutualisms where only members of species A approach B to increase the receipt of by-product benefits or in pseudo-reciprocity where A invests in B but B has no specific adaptation to behave 'cooperatively' towards B.

Alternatively, we can accept the definition of cooperation as an interaction where both parties receive invested or by-product benefits and one or both parties have an adaptation to increase the receipt of those benefits from the other.

(ii) *By-product mutualism and the snowdrift game*

The standard metaphor for the snowdrift game is the scenario where two drivers are stuck on either side of a snowdrift and both may choose to shovel or not (Hauert & Doebeli 2004). If both shovel equally each enjoys the benefit and pays half the cost of shovelling; if only one driver shovels the other enjoys the benefit at no cost but if neither shovels they cannot go home. The snowdrift game differs from the Prisoners Dilemma model of cooperation in an important way: if the opponent defects it is still better to 'cooperate'—if the other driver will not shovel the one that does will still enjoy the benefit of going home. Models of the snowdrift game show that cooperators and defectors may coexist.

A possible application of the snowdrift game is found in the territorial defence behaviour of lions (Heinsohn & Packer 1995; Doebeli & Hauert 2005). When the group is threatened by an incursion into their territory by another pride (actually simulated using playbacks) some lions charge forth while others lag behind. Some individuals were consistently laggards that avoided the costs but enjoyed the benefits of territorial defence. Lead females recognized laggards, as they were more cautious in their presence, but still led in territorial defence (Heinsohn & Packer 1995).

We might expect to see more examples of the snowdrift game 'beyond the dyad' (e.g. Gore *et al.* 2009) in cases where the benefits contributed by additional group members diminishes with group size (Hauert *et al.* 2006; see also Packer & Rutten 1988). One would expect much less laggardly behaviour by lions in small compared with large prides or when prides are threatened by larger groups. In models, we find a transition between by-product mutualism and the snowdrift game at a particular group size (Hauert *et al.* 2006).

Hauert *et al.* (2006, p. 201) consider snowdrift games to be intermediate between Prisoner's Dilemma games and by-product mutualism and emphasize that 'different dynamical domains of social dilemmas are related by continuous changes in biologically meaningful parameters'.

While accepting model continuity, I emphasize that many by-product mutualisms do not appear to be vulnerable to laggards because there is little scope for an individual to reap benefits without fully participating. A laggard that does not join a group will neither confer nor receive benefits of dilution. An individual in that group will learn of the presence of a predator

from another individual's flight, but when the tables are turned, an individual that does not flee will be eaten. A laggard cormorant that does not get in the driving line to pursue fish will not capture any or as many fish.

(b) *Pseudo-reciprocity*

Pseudo-reciprocity is simple: at some cost to itself, an actor directs assistance to another individual that increases the probability that the recipient will behave in self-serving ways that confer by-product benefits on the actor (Leimar & Connor 2003; Connor 1986). As long as the return by-product benefits exceed the original investment, the cooperative behaviour will be favoured. The simplicity of pseudo-reciprocity means that it is of little interest to theoreticians, but it may be important in nature (Clutton-Brock 2009).

The initial investment in pseudo-reciprocity need not be directed at a single individual. For example, the 'food calls' of colonially nesting cliff swallows (*Hirundo pyrrhonota*) may attract one or more nearby birds (Brown *et al.* 1991). The insect swarms the swallows feed on are ephemeral and difficult for an individual to track; but this problem is alleviated when other birds are feeding on the swarm. The feeding efforts of the new recruits enable the caller to feed longer, providing by-product benefits that more than compensate for the cost of calling.

The aid given by the actor in pseudo-reciprocity does not have to be linked to a specific return benefit either. Group-living animals often receive by-product benefits from others, and if group members are not easily replaced selection might favour providing general assistance (e.g. alarm calling) to maintain or increase those by-product benefits (Connor 1986; Kokko *et al.* 2001).

(c) *Reciprocity*

Reciprocity, or 'reciprocal altruism' (Trivers 1971) or 'score-keeping reciprocity' is now considered by most to be rare because of the stringent conditions required for it to evolve (Connor 1995a,b; Hammerstein 2003; Whitlock *et al.* 2007; Clutton-Brock 2009). More parsimonious alternatives have been offered for all of the major examples, including baboon coalition formation (Packer 1977; see Bercovitch 1988; Noë 1990), predator inspection in fish (Milinski 1987; Dugatkin 1988; see Connor 1995a and references therein) and even the classic example of blood regurgitation in vampire bats (Wilkinson 1984; see Hauser *et al.* 2009; Clutton-Brock 2009).

The most recent demonstration of reciprocity is of special interest here because it involves exchanges of help between groups rather than individuals. Krams *et al.* (2008) provided experimental evidence for reciprocity between nesting pairs of pied flycatchers in the context of predator mobbing. They randomly designated each breeding pair of a trio of nest-boxes as A, B and C, where A would be exposed to a model predator (stuffed owl) after members of B had been captured and removed. In all 41 replicates (different nest-box trios), the breeding pair from C

assisted in mobbing at nest-box A. Following the removal of the stuffed owl, the B birds were returned to their nest-box for 'phase two' where a stuffed owl was presented at nest-box B and C so A birds had a choice of which nest-box, if either, to render their mobbing services. The A birds mobbed at nest-box C in 30 of 32 trials, but remained in their own territory in the other two. In nine cases, the experimenters placed an owl at nest-box B only to compare the reactions of birds from A and C. The A birds never mobbed at nest-box B but the C birds mobbed at B in eight of nine cases. Krams *et al.* (2008) interpret these results in the reciprocity paradigm; B birds did not help at next box A so when B subsequently needed help A did not respond, thus punishing the B cheaters. The pair from nest-box C, not having suffered from B's neglect, mobbed at nest-box B except in cases where they were defending their own nest.

Russell & Wright (2008) suggested that the results of Krams *et al.* could be more parsimoniously explained as by-product mutualism. Birds mob at the nests of others for self-serving reasons: to keep the owl away from the area so it will not threaten their own nearby nest. But mobbing has costs and is less risky in the company of others. Thus, A mobbed at C's box because C's earlier efforts at A's nest were a reliable predictor that C would join in mobbing when C's nest-box was threatened. However, B's failure to show at A's nest signalled a probability that A would be mobbing alone at B's nest and that was too costly. In their response, Wheatcroft & Krams (2009) allowed that by-product mutualism could explain all of their results except for the failure of A but not C birds to mob at B after B had not helped at A's nest-box (because they had been removed). They pointed out that A would not need to rely on such signals since all birds can detect mobbing in real time at each other's nest-boxes. A would see B mobbing at B's nest-box and therefore know that they would be mobbing jointly with pair B should they go there.

Should the reciprocity interpretation of joint mobbing between pied flycatcher breeding pairs hold up, it would not only be a rare demonstration of reciprocity in non-humans but also the first demonstration of intergroup reciprocity. However, what appears to be reciprocity between dyads might effectively be reduced to reciprocity between individuals if it is shown that one particular member of each pair initiates the decision to join a mobbing event at another nest, or to remain at home. The 'decision-maker's' mate may simply be following and supporting their mate rather than engaging in reciprocity with the other group.

Before leaving this intriguing case, I will offer another by-product mutualism model that can explain all the results of Krams *et al.* (2008), including the failure of A but not C to help at B's nest-box after B birds did not mob at A's nest-box. My model assumes that mobbing at a neighbour's nest is self-serving and based on a cost-benefit decision that is almost always in favour of mobbing. The costs may, however, exceed the benefits if the birds at a nest are compromised as might be the case if they are burdened with high parasite loads or are suffering a food shortage.

High parasite loads have been shown to reduce nest defence behaviour in owls (Hakkarainen *et al.* 1998). It follows then, that the failure of the B birds to appear at nest A would be a reliable signal that the B birds were parasitized and thus joining the B birds might entail an additional cost from parasite exposure. In the case of birds weakened by food shortage, the owl will probably get them anyway so it is not worth the cost to mob there (note that in this case the putative benefit of mobbing is to deny the owl a meal so it is less likely to return rather than to just chase it away).

(d) *Parcelling*

One model that is especially interesting given the history of efforts to find examples of score-keeping reciprocity is parcelling (Connor 1992; Friedman & Hammerstein 1991; Connor 1995c). When the view is restricted to the dyad, parcelling interactions appear to be classic cases of tit-for-tat-like reciprocity. For example, when hermaphroditic black hamlets pair up to spawn, they alternate courtship displays prior to one releasing a parcel of eggs for the other to fertilize. They continue to trade parcels of eggs in a reciprocal fashion that, given the greater cost of eggs than sperm, appears to be a classic case of two-party reciprocity based on the Prisoner's Dilemma (Fischer 1988; see also Fischer 1980, 1984). But Friedman & Hammerstein (1991) and Connor (1992) argued that the division of a clutch of eggs into parcels is driven by the option to engage with other fish in the area; and those fish need not be in the immediate vicinity. Simply, if a fish offered its entire clutch to another for fertilization, the second fish could then leave to entice a third fish and thereby fertilize two clutches for the price of one. The potential of fish to 'cheat' in this fashion is limited by the two hour time window for spawning and the fact that eggs cannot be saved until the next day (Fischer 1988). By parcelling their clutch, a fish is manipulating the cost/benefit ratio of staying versus leaving for their mating partner. The harlequin seabass (*Serranus tigrinus*) apparently does not need to parcel their clutches because time constraints alone (a 30 min spawning window) are sufficient to prevent defection (Pressley 1981).

(e) *Market effects*

The opportunity to interact with a third party often creates a market which can produce profound asymmetries in the exchange of benefits (Noë *et al.* 1991; Noë & Hammerstein 1995). The investigation of market effects in the exchange of benefits has been a highly productive area but it is beyond the scope of this paper to attempt a review. The one important point to reinforce here is that market effects, such as partner choice, may be important in all the forms of cooperation discussed here (Bergmüller *et al.* 2007; Connor 2007). Individuals may choose or compete for partners that are more likely to reciprocate, that provide more by-product benefits for a given amount of investment, or that, in the exchange of by-product benefits, are less likely to be laggards. On the flip side, individuals may also choose to interact with others that are more vulnerable to being cheated

in reciprocity, that have more to invest in pseudo-reciprocity, that are more easily exploited in by-product mutualisms and that are more likely to tolerate a laggard.

(f) *Reciprocity and cognition*

Trivers (1971) pointed out that given the requirements for individual recognition, repeated interactions and memory of past interactions, reciprocity would most probably be found in long-lived social species. The difficulty of remembering past interactions and detecting cheaters lead several writers to suggest that reciprocity would be limited to a few intelligent species (Williams 1966; Hamilton 1972; West-Eberhard 1975). Important in this regard was Triver's discussion of *subtle cheating*, where one party reciprocates, but with less than expected. With the potential for subtle cheating, individuals must not only remember others with whom they have interacted and the general nature of those interactions (did they help you or not), they must also remain alert for attempts by others to 'short-change' them. This problem is also the key challenge for any attempt to explain 'non-counting' reciprocity based on other-regarding behaviour (de Waal & Suchak 2010; Jaeggi *et al.* 2010).

In contrast, Axelrod & Hamilton's (1981) Iterated Prisoner's Dilemma model suggested that cooperation based on reciprocity might be widespread, and subsequently 'tit-for-tat'-like reciprocity was 'discovered' among a range of animals that are not considered to be among the most cognitively sophisticated, including impala, vampire bats, sticklebacks, guppies, seabass and, most recently, pied flycatchers (Wilkinson 1984; Milinski 1987; Dugatkin 1988; Fischer 1988; Hart & Hart 1989; Krams *et al.* 2008). These animals take turns grooming each other, sharing blood meals, trading expensive eggs, moving towards dangerous predators and helping to mob predators at each other's nests.

Alternative explanations have been offered for all of these putative examples of non-human reciprocity, if one includes the by-product mutualism model of the pied flycatcher case presented here. The debate is far from over, however, as the alternatives, although more parsimonious, have not been directly tested, allowing even the most contested examples to enter the textbooks (e.g. predator inspection in fish; Dugatkin 2009).

Another line of research has focused on the capacity for animals that are considered to be cognitively sophisticated to engage in reciprocity (corvids and non-human primates) irrespective of whether they are known to engage in any reciprocal exchanges in the wild. Under the right experimental conditions, both blue jays and cotton-top tamarins can play tit-for-tat (Stephens *et al.* 2002; Hauser *et al.* 2003). Why then do we not see more examples of reciprocity among 'smart' animals in the wild?

Hauser *et al.* (2009) carefully considered this question and concluded that non-human animals lack both the socio-ecological pressures favouring reciprocity and sufficient integration of the cognitive capacities required to engage in score-keeping reciprocity.

Individuals have access to kin for cooperative interactions in most animal societies and the kind of situations where the fitness value of a given resource alternates between partners (thus favouring reciprocal interactions) is rare (Whitlock *et al.* 2007; Hauser *et al.* 2009). Vampire bats offer an example where the value to individuals of a given resource (blood) can vary over short periods of time and will have differing values for different individuals at a given time. Thus, a well-fed bat can surrender a given amount of blood at a cost that is much lower than the benefit received by a starving animal (measured in time to starvation; Wilkinson 1984). However, as we saw earlier, even this ‘classic’ case of reciprocity might be explained by kin selection, especially if the bats employ a ‘rule of thumb’ kin recognition rule based on association. Pseudo-reciprocity might also play a role in the bat example if group members are valuable and difficult to replace (Connor 1986; Kokko *et al.* 2001).

To engage in reciprocity, animals require several cognitive skills, including individual recognition, memory of interactions, an ability to quantify costs and benefits, to delay gratification and inequity detection (Hauser *et al.* 2009). What is surprising is that even chimpanzees, which have these abilities, do not exhibit reciprocity under experimental conditions (Melis *et al.* 2008). Hauser *et al.* (2009) argue that it is not the mere presence of the individual abilities that is requisite for reciprocity, but their integration into a single system. Humans have evolved such an integrated system, one that not only regulates reciprocity but that enables spiteful behaviour (e.g. refusing food in order to deny another food in an inequitable situation; see also Jensen 2010). Hauser *et al.* (2009) link the integrated cognitive system in humans to demands in our past to detect and punish not only cheaters but those who fail to punish (e.g. Boyd *et al.* 2003).

What kind of socio-ecological factors were at play in human evolution? Hauser *et al.* suggest that the expansion of small kin groups into larger stable groups where individuals interacted with many non-relatives lead to the evolution of reciprocity and selection to punish non-cooperating individuals.

Left unanswered to this point are the kinds of goods and services exchanged among humans and why they were sufficiently important to favour investment in the cognitive machinery to regulate the interactions. There seem to be two non-mutually exclusive candidates, and these are, not surprisingly, food and fighting.

Strong selection for a system of reciprocity and punishment of cheaters (including those who fail to punish) might derive, at least in part, from the unique human trait of cooking food. Unlike other animals, human hunters and gatherers do not generally consume food as they find it but bring food back to camps for processing and cooking: ‘this long period where food is visible to others provides great opportunity for sharing (not only of food but fire itself)’ and theft risk and may have selected not only for male–female pair bonds (Wrangham *et al.* 1999; Wrangham 2009) but more generally our system of reciprocity. It is not difficult to imagine how cooking changed

human food handling in ways that selected for the enhancement and integration of many cognitive abilities associated with reciprocity (delayed gratification, quantification of costs and benefits, cheater detection, etc).

Alexander (1989; reviewed in Flinn *et al.* 2005) argued convincingly for a prominent role for inter-group conflict as a driving force for human social complexity and intelligence, including our system of within-group cooperation and competition based to a significant extent on score-keeping and indirect reciprocity.

If Hauser *et al.* (2009) are correct, and even our closest and brainiest relatives do not engage in score-keeping reciprocity, is there any hope of finding another example, however rudimentary, of the ‘integrated cognition’ mediated score-keeping and indirect reciprocity found in humans? There are two obvious places to look; namely the other two mammalian ‘peaks’ in brain size evolution, elephants and dolphins (Connor 2007). A large number of delphinids have relative brain sizes that exceed that of any non-human primates (Connor *et al.* 1992b, Marino 1998; Connor & Mann 2006) and captive studies have revealed some impressive cognitive abilities in bottlenose dolphins (genus *Tursiops*) (Herman 2006; Marino *et al.* 2007). The most complex system of cooperative behaviour described thus far in any delphinid is the hierarchical system of male alliances found in a population of Indian Ocean bottlenose dolphins, *Tursiops* sp. (Connor *et al.* 1992a,b, 1999, 2001; Connor 2007). In the next section, I describe these alliances and the possible roles played by the various evolutionary mechanisms of cooperation (kin selection, by-product mutualism, the snowdrift game, pseudo-reciprocity and reciprocity) in mediating alliance behaviour.

3. THE DOLPHIN ALLIANCE SYSTEM IN SHARK BAY, WESTERN AUSTRALIA

(a) *Background*

The Shark Bay bottlenose dolphins (*Tursiops* sp.) have been observed for over 25 years following preliminary observations in 1982 (Connor & Smolker 1985; see Connor 2000, 2007; Connor & Mann 2006 for reviews). They exhibit a classic fission–fusion grouping pattern (Smolker *et al.* 1992) in a large unbounded social network (Randic *et al.* in preparation). A mosaic of variably overlapping individual home ranges extends beyond the 600 km² study area (Randic *et al.* in preparation). Female dolphins in Shark Bay typically begin reproducing at age 11–12, give birth to a single calf every 4–6 years and may live for 35 to over 40 years (these are very ‘chimpanzee-like’ numbers; Connor & Vollmer 2009). Females typically become attractive to males when their calves are 2.5–3 years old and are consorted by alliances of two to three males for periods lasting hours to over a month (Connor *et al.* 1996; Connor & Vollmer 2009). Consortships are initiated and maintained by male coercion of females in at least half and possibly nearly all cases (Connor & Vollmer 2009). During the year she conceives, a female will

typically be found in multiple consortships with several male alliances. The dolphins' promiscuous mating system is probably driven by sexual conflict, including the risk of infanticide (Connor *et al.* 1996; see Patterson *et al.* 1998; Dunn *et al.* 2002).

(b) *The male dolphin alliance system*

The Shark Bay males exhibit at least two nested levels of alliances. I will briefly describe these alliances and what we know about their function, and then consider the mechanisms of cooperation that might mediate these male–male relationships. Finally, I will discuss more broadly the cognitive challenges faced by the male dolphins as they cooperate to compete for mating opportunities in Shark Bay.

The first alliance level is composed of males that cooperate in pairs and trios to form aggressively maintained consortships with individual females (Connor *et al.* 1992a,b). Some male pairs and trios are highly stable within and across years. Alliance relationships between some males have lasted for 20 years (Connor 2007). Other males have much more labile 'first-order' alliance relationships, and often change alliance partners between consortships (Connor *et al.* 1999, 2001).

The majority of males also belong to teams of 4–14 males, which constitute the second level of alliance formation. Almost all consorting is conducted with males from the same team. These second-order alliances may also be quite stable; one group of seven that formed in the mid-1990s is still intact after 13 years. A group of 14 males that had 14 members in 1994 still contained 10 members 12 years later, in 2006. In a few cases males have changed second-order alliances, sometimes in association with another shift in their group or the disappearance of another member (e.g. Connor & Mann 2006).

A third level of alliance formation is suggested by associations between particular second-order alliances and joint participation in fights involving more than two second-order alliances (Connor 2007).

(c) *Possible mechanisms of cooperation in dolphin alliances*

(i) *Kin selection*

Krützen *et al.* (2003) found that males in a few of the stable first-order alliances that formed small second-order alliances were more related than expected by chance, both to their first- and second-order alliance partners. However, males in a 14 member second-order alliance were not more related than expected by chance, even to preferred alliance partners within the group. A more robust analysis of alliance membership and relatedness of over 100 males is underway. At this stage, we would characterize the mixed kinship results as indicating that kinship is one of several factors influencing alliance partner selection. A finding that relatively few males ally with close kin would not be surprising given the dolphins' slow life history; female dolphins give birth to only one calf at a time several years apart. This means that 'ready-made' alliances of close kin, such as those produced in single litters or in synchronized litters of related lions, are not possible (Packer & Pusey 1987; Connor 2007).

(ii) *By-product mutualism*

By-product mutualism probably plays an important role in the cooperation we find in first- and second-order dolphin alliances. Sexual size dimorphism is not pronounced in the Shark Bay *Tursiops* population, so it is possible that single males would be unable to coerce females into consortships. The importance of manoeuvrability in the three-dimensional habitat may also favour cooperation. When two or three males chase a female, when they are initially capturing her or after she bolts, they may spread out to either side to cut off her escape angles (Connor 2000).

The 4–14 member second-order alliances have an important defensive component. It may be important for first-order alliances with females to stay together, especially during the main breeding season, so other groups will be less tempted to attack. Connor & Vollmer (2009) suggested that this defensive need may have contributed to selection for the use of coercion in consortships. If males merely followed oestrus females, then allied first-order alliances would often find themselves moving in different directions as their females travelled to different areas to forage. Males also help defend females being consorted by other males in their group. If the males are unrelated, it is possible to invoke by-product mutualism here if unsuccessful attackers are less likely to target their group in the future.

(iii) *The snowdrift game*

During consortships, one male will often go off foraging and leave his alliance partner to guard the female (my unpublished data). This behaviour may fit the payoff structure of the snowdrift game; the temporary desertion by his partner may force the guard into doing more than 'his share' but he still benefits by guarding the female, assuming that he can mate with her.

When a pair or trio with a female is attacked by another group, the second-order alliance partners of the 'victims' may come leaping in from hundreds of meters to join in their defence. This kind of interaction is obviously vulnerable to the kind of 'laggards' we find in lions.

(iv) *Pseudo-reciprocity*

Males will help their second-order alliance partners take females from other groups. Even pairs or trios that already have a female will help a male pair or trio in their group take a female from other males, participating in the fighting and possibly even putting their own female at risk of escape or theft (Connor *et al.* 1992b). Such investment is explicable as pseudo-reciprocity if the assisting males have mating access to females consorted by other males in their group (during the other males' consortship or if they can take the female when finished with their own consortship; Connor *et al.* 1992a). Captive male bottlenose dolphins exhibit dominance relationships (Samuels & Gifford 1997) but we do not have information on dominance relationships in the Shark Bay population. However, we found a relationship between first-order alliance stability and the number of days males were observed with female consorts in one 14 member alliance (Connor *et al.* 2001) and we observed a within-group theft of a female by the most stable trio in the group.

(v) Reciprocity

Two behaviours mentioned in previous categories are obvious candidates for score-keeping reciprocity. The female guarding behaviour, while it may fit the payoff matrix of a snowdrift game, could be based on reciprocity if males take turns guarding the female. Help provided by one first-order alliance to another during a theft is also an obvious candidate for reciprocity. Time and opportunities for reciprocal exchanges are not at issue here; the males may associate with the same individuals for decades, consortships are frequent (almost constant during the main breeding season) and conflicts between groups are not rare events.

Where do we go from here? Demonstrating reciprocity in any non-human species has been notoriously difficult, dolphins are not the easiest animal to study and both of the candidate examples of reciprocity offered here have more parsimonious explanations. In spite of the difficulty, I think it is important to pursue further the issue of dolphin cooperation, but to understand why I must place the dolphin alliance system in a broader context.

(d) Cooperation, competition and dolphin social intelligence

The Shark Bay dolphins live in a very large social network (conservative estimates of the number of social relationships maintained by individuals range up to over 100; Connor *et al.* submitted), with a fission–fusion grouping pattern and a system of nested male alliances. Remarkably, the search for a comparable set of features leads more to humans than any other species (Connor *et al.* 1992a; Connor 2007).

That dolphins and humans share very large brains and large social networks with nested alliances is unlikely to be entirely coincidental. In both cases, the ability to negotiate such a large social network with a complex nested alliance system is probably related to advanced cognitive abilities.

Connor (2007) explored the cognitive challenges dolphins might face based on evidence that their alliances are not only *strategic* (simple rules such as ‘ally with your close relatives’ are not possible) but *risky* (different options yield different reproductive payoffs). This combination may put a premium on social intelligence.

Selection for social cognition will be enhanced if alliance behaviours such as guard switching and help in thefts are maintained by score-keeping and possibly even indirect reciprocity. A key in human evolution, Hauser *et al.* (2009, p. 3261) suggest, was that humans could not reliably interact with kin only: ‘the gradual expansion of small kin groups into large stable groups of unrelated individuals lead to the evolution of reciprocity, and subsequently, strong demands on the capacity to detect and punish cheaters’. The large dolphin social network with stable alliances of up to 14 unrelated males presents an obvious candidate for a human-like system of reciprocity, but we do not know if dolphins punish non-cooperators.

Two kinds of observations suggest the possibility of punishment in Shark Bay dolphins. The dolphins appear to have an ‘ownership’ rule for fish they have captured (Connor 2000). A dolphin that has caught

a prized fish will sometimes toss it repeatedly for up to 3 m then leisurely retrieve it, even when larger dolphins are present in the group. The other dolphins could clearly take the fish but do not. It would of course be interesting to see what would happen if one dolphin took another dolphin’s fish.

On a few occasions we have observed interactions where one male is simultaneously besieged by members of his own second-order alliance and sometimes members of more than one second-order alliance. These interactions involve the target male being surrounded by other males who line up ‘head to head’ with the victim before attacking or chasing him. In one case, the victim disappeared after the attacks but in the others the interaction simply ended and the dolphins carried on with normal behaviours. In no case were we able to determine what the target did to precipitate the aggression from the other males but it is possible that the victim was being punished for violating some social norm.

The cognitive challenges faced by alliance-forming males include recognizing a large number of individuals (and possibly their dominance relationships), negotiating a web of social relationships in order to gain and maintain membership in a strong second-order alliance, seeking an optimal position in that alliance for consorting females and evaluating the costs and benefits of actions at more than one level of alliance. For example, if two members of a trio evict the third they may enjoy more mating opportunities but if their action means their second-order alliance drops from five to four members then they may be more vulnerable to attack from other groups (Connor & Mann 2006).

Knowledge of third-party relationships has been touted as an important cognitive skill for social animals (Harcourt 1992) but Connor (2007) inverted this logic to highlight a phenomenon he called ‘relationship uncertainty’ as being a prominent cognitive challenge facing the Shark Bay dolphins. It is not what you know but what you don’t know about third-party relationships that presents the greatest cognitive challenge: ‘it may not be the ability to learn 3rd party relations that matters for big-brained mammals, but trying to keep track of many 3rd party relations when the size of the social network and pattern of grouping constantly introduce varying degrees of uncertainty in that knowledge’ (Connor 2007, p. 596). The dolphins’ fission–fusion grouping pattern implies that the relationships of an individual’s friends and rivals may shift when those dolphins are in other groups or ‘off camera’. Further, the dolphins’ mosaic of overlapping home ranges suggests that their knowledge of others and their relationships should lie on a continuum from animals they know well to those they know hardly at all. A male may not know if that strange male he has encountered only once before 5 years ago as a juvenile now has two or 12 adult allies.

Many point to human language as separating us from all other species because language allows us to exchange information about others in their absence. Connor (2007) outlined a simple way that dolphins could communicate about absent others that does not involve language. Bottlenose dolphins have individually distinctive ‘signature’ whistles, they can imitate the whistles of

others, and whistles carry information other than identity (reviewed in Janik 2009). Thus, if a dolphin produces a copy of another individual's signature whistle and includes modifications that convey affect, then a simple but very powerful mechanism is available to dolphins to communicate about others in their absence.

The study of the Shark Bay dolphin alliances generates insights not only into dolphin society but also helps us think about human social cognition in new ways. For example, the challenges to humans of negotiating a system of nested alliances may have been underexplored. The nested dolphin alliances may also bridge ideas about demands on social cognition between two very different camps: primatologists focused on alliance formation and social relationships within non-human primate groups (e.g. Harcourt 1992) and those interested in the role intergroup conflict played in the evolution of human intelligence (Alexander 1989; Flinn *et al.* 2005; Connor & Mann 2006).

To return to the question of whether we should pursue further studies of dolphin cooperation and social cognition given the difficulties of doing so, I think the answer is strongly in the affirmative. If Hauser *et al.* (2009) are correct, then even our closest relatives lack the integrated cognitive systems that we use to mediate cooperative relationships based on score-keeping and indirect reciprocity. Dolphins may be the last and best hope for finding such a system in another species. The ultimate features that Hauser *et al.* (2009) suggest drove the evolution of the human system are present in dolphins, which also have the second largest relative brain size after humans.

Unfortunately, research on dolphin cognition and social systems has the blessing and the curse of being interesting to many disciplines (biology, psychology, anthropology and even political science) but at home in none. Dolphin researchers are rare in biology and psychology departments and absent in anthropology, whose mission to discover what is unique about humans has, for historical reasons, focused exclusively on homology and divergence (studies on great apes and other primates) rather than convergence. The popular 'Mind, brain and behaviour' initiatives on research campuses do not offer much hope, as they are usually cobbled together from the core departments and fail to include a field component. Given the degree to which academic divisions are fossilized, progress might depend on a greater commitment to dolphin cognitive and behavioural research from non-academic institutions that have captive dolphins for public display and education.

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