REVIEW

Cooperation experiments: coordination through communication versus acting apart together

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Over the last two decades a large number of experiments have been conducted in which two conspecifics, mainly vertebrates, could obtain rewards through cooperation. At least three different motivations to perform such experiments can be distinguished: (1) detecting the mechanistic basis of naturally occurring forms of cooperation; (2) analysing behavioural strategies specific to cooperation; and (3) testing game-theoretical models. Experimenters in the latter two categories, on which this review concentrates, make use of highly artificial devices. The impression of cooperation in the third category is created because two animals are tested simultaneously after having been trained to interact with an apparatus individually before the experiment. These results can be explained most parsimoniously as the product of instrumental ('trial-and-error') learning, hence my label 'instrumental cooperation'. The underlying philosophy of several studies is reminiscent of the strongly disputed ideas of the 'behaviourist school'. Results from experiments in the second category highlight the importance of communication; therefore I call this 'communicative cooperation'. The crucial role of communication identified by studies in the second category calls into question the relevance of the most popular paradigm used in the third category, the two-player Iterated Prisoner's Dilemma. Its stringent conditions, which are hardly ever fulfilled in nature, are very difficult to fulfil in experiments too. I propose that future studies concentrate on experiments that emphasize the role of communication and partner choice with the aim of explaining the emergence and maintenance of naturally occurring forms of cooperation.

Cooperation is a phenomenon that has attracted interest from scholars of many different disciplines, some of which concentrate on human behaviour (psychology, sociology, anthropology, economics), while others focus on interactions among nonhuman organisms (ethology, behavioural ecology, evolutionary ecology). An exchange of ideas, which is no doubt in the interest of all these disciplines, is hindered by a confusion of tongues that is reminiscent of the tower of Babel. This confusion, a consequence of different traditions, different jargon and different goals, is most notably apparent where disciplines overlap. For example, experiments in which two animals must cooperate to obtain a reward have been conducted by people with backgrounds in comparative psychology,

ethology and behavioural ecology. At first sight, the objectives and methods of these studies seem very similar, but under close scrutiny fundamental differences become apparent. My main goal here is to point out explicitly what these differences are. To do so, I reflect on why cooperation is such an enigma for so many different disciplines. This is not possible, however, without first resolving the terminological confusion mentioned above. My secondary goal is therefore to reduce confusion by proposing a drastic simplification of the jargon used. I hope this helps to remove some of the roadblocks between my own discipline (behavioural ecology) and related fields.

Terminology

Most of us will have an intuitive idea of what is meant by 'cooperation', but chaos reigns in the terminology used. The most commonly used terms (cooperation,

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mutualism, reciprocity, reciprocal altruism and symbiosis) are sometimes used as synonyms, sometimes as categories in a hierarchical system and sometimes to denote mutually exclusive categories. The definitions and descriptions that have been proposed can be classified on the basis of two dichotomies: (1) form–outcome and (2) individual contributions–(series of) interactions (Fig. 1). I give a few examples of current usage of terms below.

Bronstein (2003), an ecologist specialized in interspecific interactions, defines the terms cooperation, mutualism and symbiosis as mutually exclusive categories: cooperation is defined as a mutually beneficial interaction between conspecifics, while the terms mutualism and symbiosis denote similar relationships between members of different species. Symbiosis applies to all forms of intimate and long-term interactions, whereas mutualism refers only to interactions of short duration. The terms used by Bronstein and most other ecologists are descriptive and based on form as well as the 'usual' outcome. Ecologists tend to express gains and losses in proximate terms (e.g. units of time or energy, nutritional value, etc.), but sometimes use proxies of fitness such as changes in number of offspring.

De Waal (2000), a primatologist, uses the term 'mutualism' to distinguish interactions that yield benefit for two participants simultaneously from series of interactions in which participants take turns in giving and receiving benefits, which he calls 'reciprocal altruism' after Trivers (1971). De Waal then uses 'cooperation' as an overarching category. This differs from my own terminology used in connection with coalition formation in baboons (Noë 1990) and biological markets (Noë 2001): I used 'cooperation' to denote interactions with immediate benefit for all participants involved (de Waal's mutualism) and 'reciprocity' as an overarching term for any series of cooperative and altruistic interactions that yields a net benefit for all participants at the end of the series. I defined 'mutualism' and 'symbiosis' in the same way as Bronstein above (Noë 2001). Both de Waal and I failed to make clear whether our definitions were based on form or outcome. In contrast, Boesch & Boesch (1989) defined cooperation purely on the basis of form, distinguishing increasingly complex categories of cooperative hunting behaviour in chimpanzees: similarity, synchrony, coordination and collaboration. These terms describe the movements of the hunters relative to each other in time and space.

For Dugatkin (1997), a behavioural ecologist specialized in game theory, 'reciprocity' is one of several mechanisms that can lead to 'cooperation', which for him is defined as 'an outcome that — despite potential relative costs to the individual — is 'good' […] for the members of a group, and whose achievement requires collective action' (Dugatkin 1997, page 14). Thus, Dugatkin's 'reciprocity' equals de Waal's 'cooperation'. He explicitly uses the term 'to cooperate' to refer to the behaviour of individuals, but the definition hinges nevertheless on the outcome of interactions between two or more individuals.

Bowles & Gintis (2003, pp. 429–430), two economists, define cooperation as 'an individual behaviour that incurs personal costs to engage in a joint activity that confers benefits exceeding those costs to other members of one's group'. This is how many biologists would define 'altruism'. Sachs et al. (2004), a group of evolutionary ecologists, also define cooperative interactions as consisting of one or more acts that are costly to one self and beneficial to one or more other individuals. In both papers the definition used is thus based on the outcome of individual behavioural strategies.

Thus, for some, 'cooperation' is a certain type of interaction that can be recognized by form and/or outcome, whereas for others it is a strategy used by a participant in an interaction, and for yet others it is a characteristic of a long-term relationship. Several of the other terms listed above, such as mutualism and reciprocity, are used in multiple ways too. A different use of labels is not, in itself, a cause for concern, but this cacophony of terms may obscure the fact that the same term used in two studies stands for two fundamentally different phenomena or, vice versa, the same phenomenon carries different labels in different publications. This notably hampers the interpretation of differences in outcome of cooperation experiments. In what follows I stick to the terms the authors of the reviewed studies used themselves unless I cannot rely on the context to avoid confusion.

	Individual contributions	(Series of) interactions
Form	Behavioural, physiological and/or morphological strategies of individual participants	Associations in space and time between contributions of individual participants
Outcome	Accounts of gains and losses resulting from strategies used by individuals	Accounts of gains and losses of individual participants in relation to each other

Figure 1. Classification of definitions. Definitions and descriptions of cooperation, reciprocity, mutualism, reciprocal altruism and symbiosis can be classified by two dichotomies. This review advocates the use of definitions falling into the upper-left cell.

Why Cooperation is Often, But Not Always, a Puzzle

Cooperation takes many forms that can be classified along different dimensions (reviewed in Connor 1995a; Sachs et al. 2004; Bshary & Bronstein 2005). The most important theoretical distinction is between cooperation among close relatives and cooperation in which genetic relationships cannot play a role. The latter can be split further into interactions between conspecifics and interactions between heterospecifics. Further distinctions can be made on the basis of the number of interactions between the same participants and the number of individuals that interact. The dynamics of one-off interactions and of finite series of interactions are different from open-ended series of interactions (Gintis 2000). Collective action problems (in which more than two, and usually many, partners have to contribute simultaneously: Nunn & Lewis 2001; Ostrom 2001), and biological markets (in which individuals can choose among multiple partners: Noë & Hammerstein 1994, 1995), tend to have a much richer strategy set than two-partner interactions.

Cooperation attracts so much attention because its emergence and maintenance, both on an evolutionary timescale and on the timescale of individual relationships, can form quite an enigma. The hardest theoretical nut to crack remains cooperation between unrelated individuals. The art of cooperation consists of investing the right amount in the right partner at the right moment. One should avoid 'greedy' individuals that may try to reap short-term benefit by not returning favours, but one should also avoid being so 'mistrustful' that cooperation breaks down or never starts.

In many cases the benefits of cooperation to an individual can be reaped only if that individual invests first. The returns may be considerably larger than the investments, but there is almost always a risk that the returns never materialize. It is often suggested that this risk is considerably higher if returns are delayed, but the importance of the distinction between 'immediate' and 'delayed' returns tends to be overrated. What counts is the amount of control over the partner between the moment of investment and the moment of receiving the returns. High degrees of uncertainty can exist when commodities are directly swapped, for example for a subordinate monkey swapping a grape for a piece of apple with a dominant. Low degrees of uncertainty can go hand in hand with long delays, for example a plant growing a food body may attract ants weeks later, but it is protected as long as the ants walk on the plant to consume the food bodies. Theoretically there is no uncertainty if commodities are swapped simultaneously and neither party can retrieve (part of) its investment after a done deal, but I can think only of examples of human interactions that are embedded in many safeguards, such as cold war exchanges of spies at border posts.

Not all forms of cooperation need to have this element of strategic dilemma, however. Natural selection may have resulted in mechanistic solutions. Some flowers, for example, have structures that make it (almost) impossible for an insect to obtain nectar without taking on pollen. Such a fail-safe 'hardware' solution is required because the flowers invest long before they get the returns. Such interactions would not qualify for the label 'cooperation' according to the definition Bowles & Gintis (2003) proposed for human behaviour (see above). However, in the rest of this paper I concentrate on behavioural strategies that can either be 'preprogrammed' (also called 'hardwired') conditional strategies, or strategies determined by cognitive processes such as trial-and-error ('instrumental') learning, observational learning, insight and so forth. I also limit the discussion to experiments in which conspecific vertebrates interact.

Why Definitions Should be Formulated in Terms of Individual Strategies

I assume that strategies that prevail in real-time interactions between individuals have the properties of evolutionarily stable strategies (Maynard Smith 1982). Selection takes place at the level of individuals (or in rare cases, not relevant to this paper, at the level of units consisting of several individuals), but not at the level of interactions or relationships between individuals. Definitions of cooperation are therefore best phrased in terms of strategies of individuals, whereby a strategy can contain behavioural, morphological and physiological elements. Selection leads to strategies that *as a rule* increase the fitness of the individual. This means that a strategy is identified by its form, while its function becomes apparent only as the average outcome of many events. Consider, for example, two lionesses that increase their average hunting success by stalking and chasing zebras in a coordinated fashion. It is not necessary for every coordinated hunt to yield higher fitness than every solitary hunt. Sometimes cooperative hunts will fail and sometimes a lioness will succeed in killing a zebra on her own. One seeks the explanation for 'coordination behaviour' because its apparent function is to improve the chances of successful hunts. One does not look for a different evolutionary explanation for coordination behaviour in hunts that fail.

The two lionesses both invest and both obtain something in return if the hunt is successful. The lionesses also invest in their interaction with the zebra and, when successful, get its body parts in return. Nobody will call the latter interaction 'cooperation', however, because the zebra invests only to prevent benefits for the lionesses. Cooperative behaviour thus entails investment in another individual that makes it more likely that the receiving individual changes its behaviour in favour of the investor. In most cases this investment will be beneficial to the receiver, while receivers are under selective pressure to avoid interactions unless they are beneficial to them.

There are two exceptions: (1) when investments have no fitness consequences for receivers and (2) when interactions are costly, but avoiding interactions is more costly still. The first exception was labelled 'by-product mutualism' by West-Eberhard (1975): X interacts with Y to obtain a commodity that Y would produce independently of X's behaviour. A related concept is 'pseudoreciprocity' (Connor 1986): X invests to make Y produce more of

a commodity, but this does not result in higher costs for Y. The second exception can be the result of X imposing costs on Y whenever Y does not cooperate. This can take the form of 'harassment' or 'punishment'. Harassment aims at obtaining immediate benefits: it stops when the harassed individual capitulates (Stevens & Stephens 2002) and is observed notably in the context of food sharing (Stevens 2003; Stevens & Gilby 2004) and mating (Smuts & Smuts 1993; Clutton-Brock & Parker 1995a). In practice, harassment can be hard to distinguish from other forms of forceful appropriation of commodities, such as grabbing pieces of food from the hand or mouth of the victim, or rape. Punishment is used to change the future behaviour of the partner in favour of the punisher (Clutton-Brock & Parker 1995a, b). It normally takes place *after* a frustrating interaction and, in contrast to harassment, can yield only delayed benefit. The effect is comparable to that of negative reinforcement in learning experiments. Punishment and reciprocal altruism (Trivers 1971) both imply repeated interactions between the same individuals and investment in future benefits that can be reaped only after a certain delay. Such strategies are less likely to evolve than those that result in immediate benefits because animals tend to discount the future rather strongly (Clements & Stephens 1995; Stephens 2000; Stephens et al. 2002). Strategies aimed at immediate returns can also have an effect on future interactions, of course. Harassment and punishment boil down to obtaining benefits from other individuals by the use of force. No other interactions with the same characteristic, for example predation, parasitism and aggressive competition, are called 'cooperative'. Interactions that follow harassment or punishment may have the characteristics of cooperation, but only when seen in isolation. It is therefore questionable whether it makes sense to discuss such strategies in the same breath as mutually beneficial relationships. I nevertheless review one experiment in which harassment played a crucial role because it tells us something about the problem of partner perception.

A Simple Set of Terms

The considerations listed above have led me to propose a greatly reduced set of terms that can be used to describe all forms of mutually beneficial interactions and relationships as well as the individual strategies from which they result.

(1) 'Cooperation': all interactions or series of interactions that, as a rule (or 'on average'), result in net gain for all participants. The term includes all other terms that have been used for mutually rewarding interactions and relationships: reciprocity, reciprocal altruism, mutualism, symbiosis, collective action and so forth. Examples of cooperative interactions are coalition formation, pollination by insects and formation of mycorrhiza.

(2) 'Cooperative investment': all behavioural, morphological and physiological expenditures that, as a rule, facilitate cooperation. Considered in isolation a cooperative investment results in a loss of fitness. The difference between this and 'altruism' is that it need not result in a benefit for another individual. Examples are giving warning calls, supporting a group member in a fight, growing food bodies and detecting deception.

(3) 'Cooperative returns': all profits that an individual receives as a direct result of its 'cooperative investments'. Investments and returns can be expressed in different currencies (fitness for evolutionary biologists and utility for economists) but also in proximate terms such as quantities of energy, food, money and so forth. Examples are saving close relatives through early warning, receiving support from an individual in which support was invested, receiving protection from ants attracted by food bodies and avoiding losses caused by deception.

Mechanisms Relevant to Cooperation

Three questions require an answer. (1) What mechanisms are needed to perform well in 'natural' cooperative interactions with an unrelated individual? My conception of 'nature' is very broad here. I refer to interactions in any form, as long as they occur spontaneously somewhere in this world and not only in artificial contraptions set up by an experimenter. (2) Which of these can realistically be expected to occur in view of constraints on physical and cognitive abilities? (3) Which of these are specific to cooperation? Above I explained why it is the form of individual strategies that provides the defining features of cooperation rather than the outcome of such strategies/interactions. This also implies that interactions qualify as cooperation only if at least one participant uses at least one mechanism specific to cooperation. I will go back to my hunting scenario to explain this. When two lionesses target the same zebra independently but simultaneously, this is likely to increase the chance that one of them catches the prey. However, in the absence of mechanisms that improve coordination between the lionesses, or ensure sharing of the carcass without damaging fighting, nothing differentiates their behaviour from foraging. In other words, there is no behavioural mechanism that guarantees that both lionesses *on average* benefit from hunting the same prey simultaneously. Of course, when such simultaneous hunts occur often enough by chance, selection for behaviour that improves coordination is possible. Such behaviour could even emerge during the lifetime of two lionesses through learning processes.

Theoretical Models of Cooperation

An individual can improve its net benefit from cooperation by: (1) lowering the production costs of its own investment; (2) inducing a favourable change in the behaviour of the partner; and (3) switching to a more profitable partner. Option 2 is a core element of 'partner control' models, while option 3 is the essence of 'partner choice' models (Bshary & Noë 2003), which are discussed below.

'Partner control' models, most of which are based on the two-player Iterated Prisoner's Dilemma (IPD), stress the importance of mechanisms that ensure a continuation of net gain, or an improvement in net gain, in a series of interactions with a specific partner. This means that participants must somehow adjust their behaviour

conditional upon fluctuations of their returns that co-incide with changes in the partner's behaviour. One can also imagine 'bookkeeping' of payoffs to one's self and one's partner, but the ability to do so may be limited to humans (Brosnan & de Waal 2002) and, even in humans, cognitive constraints limit its scope (Milinski & Wedekind 1998). Abandoning the partner is the only sanction avail-able in classical IPD-based models. However, several varia-tions on the same theme have been proposed, such as investing slightly more or less depending on the partner's behaviour (Roberts & Sherratt 1998). Other models also consider punishment and harassment, as described above.

De Waal (2000; see also de Waal & Luttrell 1988; Brosnan & de Waal 2002) calls bookkeeping strategies 'cal-culated reciprocity'. He contrasts this with two other mechanisms that would lead to stable cooperation with-out the need to keep score mentally: 'symmetry-based rec-iprocity' and 'attitudinal reciprocity'. Reciprocity is symmetry based when animals, for example, share food preferentially with group members with whom they have a 'symmetrical' relationship, because they are either close associates (i.e. the symmetry lies in the fact that they are often in each other's proximity) or relatives. De Waal (2000, page 260) describes 'attitudinal reciprocity' as fol-lows: 'Attitudinal reciprocity follows from variability in so-cial predispositions, ranging from friendly to hostile, and a tendency to adjust to the predisposition perceived in the other: if individual A acts friendly towards B, this stim-ulates B to act friendly towards A'.

Thus, both of these latter forms of reciprocity are based on differences in attitude towards group members. I take issue with de Waal's (2000) suggestion that kin relation-ships provide examples of symmetry-based reciprocity. Ac-cording to Hamilton, the coefficient of relatedness, r, between any two individuals will be the same both ways (at least in vertebrates). Furthermore, the coefficient of re-latedness is also the same both ways for unrelated animals, namely zero. However, the average benefit, B, from receiv-ing a cooperative investment, the average cost, C, of pro-ducing such an investment, and thus the value of the term (B/C) in Hamilton's inequality $(B/C) > 1/r$ will rarely be the same (Hamilton 1964). The term B/C can also fluc-tuate strongly over time. The idea of symmetry based on proximity is also puzzling, since proximity is by definition symmetrical for all pairs of animals in a group in absolute terms. The more direct term 'proximity-based' reciprocity would have been less problematic.

In 'attitudinal reciprocity' the attitude taken towards a specific individual changes over time depending on an animal's interactions with that individual. It thus seems to be a modulating force on 'symmetry-based reciprocity', but otherwise I fail to see a principal difference; a change in 'attitude' towards an individual is very likely to result in a change in the amount of time spent in its vicinity, which would blur the distinction between the two concepts. De Waal may have had in mind changes in attitude that are specific to experiences that are, or could have been, co-operative, but that would bring us back to the idea of bookkeeping. One could, however, ponder about the degree of fuzziness that bookkeeping mechanisms could have, or should have, to maintain cooperative relationships.

'Partner choice models', which include extensions of the IPD-model (Batali & Kitcher 1995; Ashlock et al. 1996; Roberts 1998; Dugatkin & Wilson 2000) and the biological markets paradigm (Noë & Hammerstein 1994, 1995), put the emphasis on the option of choosing and switching partners. The stress is not on bookkeeping of past interac-tions, but on choosing the best offer momentarily avail-able. The presence of alternative partners can provide leverage over the current partner, even in the absence of an actual switch. Choosing partners implies a number of mechanisms well known from sexual selection theory: judging the partner's quality, a memory for the partner's quality and location, searching strategies, judging the honesty of signals and so on.

Most published experimental studies of cooperation exclude the possibility of partner choice and partner switching, although these are crucial to most natural forms of cooperation and mutualism. Examples of natu-rally occurring cooperation restricted to two participants are rare (reviewed in Noë 1992; Bronstein 1998; Hoeksema & Bruna 2000; Wilkinson & Sherratt 2001; Ferrière et al. 2002; Simms & Taylor 2002; West et al. 2002; Bshary & Noë 2003; Hammerstein 2003; Sachs et al. 2004; Bshary & Bronstein 2005). The limitation to two interacting sub-jects may sometimes be chosen for practical reasons, but more often it is based on the explicit or implicit assump-tion that cooperating individuals are locked in a standard two-player IPD.

One could argue that the impression that two by two cooperation is rare in nature is due to the way in which the label 'cooperation' is used. For example, the agree-ment of territorial neighbours on the location of a mutu-ally respected border (Whitehead 1987; Hyman 2002) is usually seen as 'conflict resolution', but it fulfils the crite-rion of cooperation: the fitness of both neighbours in-creases compared to a situation in which they fight during each encounter. One obviously cannot choose or switch a neighbour (but see Greene et al. 2000 for an inter-esting exception). Cooperation and conflict are two sides of the same coin and it is a matter of taste to which side more attention is given.

Three Motivations for Doing Cooperation Experiments

I recognize three fundamentally different motives to conduct cooperation experiments with captive animals.

Motive 1: analysing naturally occurring cooperation

The goal is to understand the stability and maintenance of naturally occurring instances of cooperation by reconstruct-ing the essential elements of the natural situation as faithfully as possible in the laboratory. Laboratory experi-ments are often complemented by experiments in a natural setting. This category is the domain of people working with an enormous diversity of interspecific mutualisms, for example ant-protection mutualisms, mycorrhiza, pollina-tion, seed dispersal and so forth (reviewed in Bronstein 1998; Simms & Taylor 2002; Sachs et al. 2004; Bshary & Bronstein 2005). In contrast to the following two categories,

mechanisms in this category are often considered to be species specific. Research starts from a plethora of observed phenomena, which is reduced to a smaller, but heterogeneous, set of underlying strategic principles (Bshary & Bronstein 2005). Quantification of cooperative investments and returns, for example in the form of exchanges of nutrients, is often the goal of experiments, whereas experimenters typically attempt to control these parameters in the studies belonging to the categories reviewed below.

In comparison, reports of cases of cooperation among unrelated conspecifics are rare (Noë & Hammerstein 1995; Hammerstein 2003; Stevens & Hauser 2004). Some well-studied examples, for example cooperative hunting and coalition formation, are difficult to study experimentally in a laboratory setting. The best-known laboratory studies are probably those on blood regurgitation in vampire bats and predator inspection in fish. A considerable body of work on predator inspection by Pitcher and colleagues (Pitcher et al. 1986; Pitcher 1992; Murphy & Pitcher 1997) and Brown and colleagues (Brown & Godin 1999; Brown et al. 2000; Brown & Dreier 2002; Brown & Magnavacca 2003) was directly based on observations in the wild and aimed at understanding mechanisms and function without a priori assumptions about correspondence with specific game-theoretical paradigms. Other studies were aimed at testing theoretical models and thus fall under my 'motive 3' below (vampire bats: Wilkinson 1984; DeNault & McFarlane 1995; predator inspection: reviewed in Dugatkin 1997, pp. 63–70).

Motive 2: identifying proximate mechanisms

The assumption that the proximate mechanisms used are largely independent of goal and context justifies studying cooperation under artificial circumstances. Furthermore, mechanisms are often implicitly assumed to be common to many species and taxa independent of phylogeny, in line with the tenets of comparative psychology. These assumptions imply that laboratory tests with animals provide valid models for human cooperation, the secrets of which many researchers in this group seek to unravel.

Motive 3: testing game-theoretical models

Studies in this category consider a much broader group of organisms than those under 'motive 2' and assume that strategic principles, rather than proximate mechanisms, are general. Members of different species are assumed to implement the same strategies when confronted with equivalent problems, but use species-specific mechanisms to do so. The emphasis in experimental design is on the translation of strategic options and payoff configurations into behavioural choices and rewards. Cooperation is defined by the economic outcome of a pair of choices made by two different individuals.

EXAMPLES OF COOPERATION EXPERIMENTS

I limit myself to a discussion of experiments based on motives 2 and 3, since the majority of 'motive 1' experimental studies deal with interspecific cooperation and fall beyond the scope of this review. I do not attempt to pigeonhole all the cooperation experiments ever performed into these categories. Instead, I have selected some representative studies of each.

Motive 2: Identification of Mechanisms

The capuchin experiments

A classic cooperation experiment was first conducted by Crawford (1937): two chimpanzees had to pull on two ropes simultaneously in order to move a crate containing food towards their cage, which was too heavy for a single individual to achieve alone. They did not succeed until Crawford first trained them separately to pull when she shouted: 'Pull!'. When placed together again, the chimpanzees proceeded to pull simultaneously, only on Crawford's command at first, but after a while without the external cue. However, they did not transfer their 'knowledge' to a similar situation in which the ropes dangled from the top of the cage (see discussion in Tomasello & Call 1997).

Two teams have conducted experiments with capuchin monkeys using Crawford's basic paradigm, but implemented in very different ways. The two teams arrived at almost opposite conclusions. In the first team (Chalmeau et al. 1997; Visalberghi et al. 2000), pairs of monkeys had to pull two small levers simultaneously to get food. In the 1997 study, the food fell from a tube halfway between the levers; in the 2000 experiment, it fell near each of the levers. In contrast, the capuchin monkeys in the second team's experiments (Mendres & de Waal 2000; de Waal & Berger 2000; de Waal & Davis 2003) could obtain food rewards by simultaneously pulling on two iron bars attached to a tray with food cups. The tray was counterweighted in such a way that a single individual could not pull it towards the cage. Mendres & de Waal (2000) studied explicitly the influence of communication by using both opaque and transparent screens to separate the monkeys.

In all experiments the capuchin monkeys succeeded in obtaining food by acting simultaneously. However, both Chalmeau et al. (1997) and Visalberghi et al. (2000) concluded that success was not due to any form of coordination between the subjects, but was based only on chance occurrence of simultaneous pulling. Mendres & de Waal (2000) explained the improved coordination of their subjects by the fact that their apparatus resembled a natural feeding situation, such as pulling a branch with fruit towards themselves. They showed explicitly that acting in a coordinated manner required communication. A test conducted with an opaque separation wall, which had a small hole in it to ensure that the subjects were aware of each other's presence, showed that the monkeys were significantly less successful in coordinating their pulling behaviour if they could not see each other. They were not able to improve coordination on the basis of the movements of the tray resulting from the partner's attempts alone.

The capuchins in the study of de Waal & Davis (2003) were not separated by a partition. They thus had to reckon with partners that would be able either to monopolize or

to share food. Food was offered in two ways: 'clumped' or 'dispersed'. The results show that their decision to cooperate depended on certain characteristics of their partner: they cooperated with subordinates under all conditions, but with dominants only when the food was dispersed. They more readily cooperated with relatives than with nonrelatives. The fact that they made these distinctions from the first trials on shows that expectations about the behaviour of their partner played a role in their decisions.

Mendres & de Waal (2000) referred to the cooperative hunting behaviour of capuchins observed in nature to suggest that the behaviour shown by their subjects reflected natural behaviour, as opposed to behaviour that can be acquired only by extensive training. This claim seems justified only if one accepts the idea that the same cooperative mechanisms are used in different forms of cooperation. I agree that the behaviour used in their apparatus resembles elements of natural foraging behaviour, but the essential observation would be that animals pull branches to themselves in a coordinated fashion under natural conditions. To my knowledge this has never been observed.

Experiments with cottontop tamarins

Hauser et al. (2003), studying cottontop tamarins, found that one member of a pair could pull an L-shaped tool towards itself and provide food for its partner only, for itself only, or for both animals at once. In some experiments the animals were separated by a mesh partition, but they could always see each other and communicate vocally. Hauser et al. worked with pairs of untrained animals, as well as pairs consisting of an untrained subject and one of two stooges that were trained to perform the same behaviour consistently: one 'altruist' and one 'defector'. Hauser et al. acknowledged that the use of a single 'altruistic' and a single 'defecting' stooge amounts to pseudoreplication. This is a serious problem because the paper's main result hinges on the behaviour towards the altruist stooge. It is obvious, however, that training several stooges is difficult and time consuming.

The cottontop tamarins were more likely to pull when paired with the altruistic stooge than with the defector. As Hauser et al. remarked, this result can, at first sight, be explained as a simple reinforcement effect. However, three further tests were done to differentiate explicitly between behaviour elicited by the food rewards per se and behaviour in reaction to the way in which the partner produced those food rewards. A first experiment was run with pairs of untrained subjects. After multiple tests in which pulling by the partner was the only way to obtain a reward ('altruistic pulling'), a series of trials followed in which each pull resulted in a reward for both. Hauser et al. claimed that food received from the partner in this latter series was perceived as a by-product of egoistic behaviour, as opposed to food received through altruistic pulling, and that the 'simple reinforcement' hypothesis would predict an increase in pulling in a subsequent series of altruistic pulling. The pulling frequency was indeed higher than in the earlier series of altruistic pulling, but not significantly so (Figure 4 in Hauser et al. 2003). I agree that this makes

the 'simple reinforcement' explanation unlikely. The justification is weak, however, because it is based on a test of the null hypothesis, namely that no difference is expected between the series before and after the intermezzo of 'egoistic' pulling.

In a second experiment, again with untrained individuals, one animal could obtain one piece of food and give three pieces to her companion by pulling the L-shaped tool. In alternating rounds the companion had the opportunity to give two pieces in return, but received nothing herself. Given the latter role, the tamarins almost never pulled, in contrast to the experiment in which they alternated with the 'altruistic' stooge described above.

A third experiment showed that the animals were not inclined to act more altruistically when a passive tamarin sat next to them and an experimenter pushed the food into their reach, thus rewarding the subject in the same way that an actively altruistic partner would have done. This led Hauser et al. to conclude that signs of willingness to behave altruistically have to come directly from a conspecific in order to elicit altruistic behaviour. Taken together, I see these results as strong support for the idea that cooperation should be defined on form, not outcome, since form is apparently more important than outcome, at least for these tamarins.

In Cronin et al.'s (2005) study cottontops, which sat facing each other separated by a transparent partition, could obtain a reward simultaneously by pulling a handle simultaneously. The study concentrated on one aspect of cooperation: coordination. Cronin et al. (2005, page 140) saw their results as support for the finding of Mendres & de Waal (2000) and Hauser et al. (2003) that 'tamarins are sensitive to the need of a partner in order to successfully solve the task'. This conclusion is based on the fact that the subjects pulled much more frequently in the presence of a partner than in its absence. However, the same effect could probably have been achieved by combining the opportunity to gain a reward with a red light or other cue. The results of Mendres & de Waal (2000) and of Hauser et al. (2003) are, in fact, very different in quality. By comparing the effect of an opaque partition with a mesh partition containing a small hole, Mendres & de Waal could show that it is not the presence of the partner that gives the essential cue, but that the animals have to see each other to coordinate well. Hauser et al. showed explicitly that it is not the presence of the partner, and not even what it does (pulling an L-shaped tool), that makes the difference, but the conditions under which it pulls the tool.

Coordination is an important proximate mechanism needed to accomplish cooperation. By putting emphasis on this aspect of behaviour, the study of Cronin et al. resembles studies of rodents that have to coordinate movements in order to obtain a reward ('shuttling experiments', see Schuster & Perelberg 2004, and references therein), rather than the primate cooperation experiments cited in the study and mentioned above.

The role of harassment in an experiment with keas

In an experiment conducted by Tebbich et al. (1996) with keas, large parrots from New Zealand, two

individuals had to perform different tasks in order to obtain a reward. By sitting on a seesaw, a bird could lift the lid of a box with a food reward, but the lid closed as soon as the bird left the seesaw. Consequently, a single individual could not gain access to the reward by a lone effort. Two partners could both gain either by taking turns (i.e. reciprocal altruism as defined by Trivers 1971), or by sharing the food. In contrast to the experiments described above, the birds could spontaneously choose their partners from among their six cagemates.

No interactions, or series of interactions, ended in a benefit for both partners. Instead, only dominant individuals obtained rewards, manipulating subordinates to remain on the seesaw by behaving aggressively whenever subordinates attempted to do anything else. The dominant keas thus behaved like animal trainers who shape behaviour using negative reinforcement. This provides a good example of harassment with an immediate reward for the actor.

Motive 3: Testing Theoretical Models

The blue jay experiments

The experiments of Stephens et al. are based on a two-player game-theoretical paradigm and exemplify studies in which cooperation is defined by outcome. Clements & Stephens (1995) tested three pairs of blue jays. They placed a bird in each of two adjacent test chambers, each of which was essentially a Skinner box with two keys: one served as a 'cooperate' (C) key, the other as a 'defect' (D) key. In response to the combination of pecks given by the two jays, food pellets dropped into separate food cups, one in each compartment. In one experiment the number of pellets was such that the birds were confronted with an IPD and in another they played a 'mutualism-game' (cf. West-Eberhard 1975) in which the C–C combination gave the highest payoff. The tests were conducted with either an opaque or transparent partition between the two chambers, but the authors did not report whether this made any difference.

Stephens et al. (2002) used a comparable apparatus, but the pecking keys of the 1995 experiment were replaced by a C-perch and a D-perch on which the birds had to land to make their choice. The experiment itself differed in two important ways from the 1995 experiment. (1) The payoff configuration per round was the same as in the 1995 IPD experiment, except that the birds could see the food pellets accumulating in a transparent tray and could eat them only after making four choices. Below I argue that this in fact changes the payoff configuration in a crucial way. (2) One bird was used as a 'stooge', that is, the experimenters determined its 'choices'. Thus, the subject actually played against a machine, but could see a conspecific at work in the adjacent test chamber. Compared to the study of Hauser et al. (2003) the role of the stooge was very different: in the tamarin experiment a different stooge showing different behaviour was consistently connected with different rewards, which were independent of the subject's strategy, whereas, in the blue jay experiment, rewards

could vary even though the behaviour of the stooge and subject remained the same.

Predator inspection in fish

'Predator inspection', the approach of a predator by a prey that is aware of the predator's presence, is best known for fish, but also occurs in other species (e.g. antelope: FitzGibbon 1994). It is often performed in a coordinated manner, usually by two, but sometimes more, individuals. Predator inspection was proposed as a test of the two-player IPD by Milinski in his seminal paper of 1987. The motive for the experiment was not to analyse the function of predator inspection as such, although this was only partially understood at the time. I describe only briefly the basic idea of Milinski's well-known experiment, which has since been repeated many times by several other authors. I refer the reader to Dugatkin (1997, pp. 59ff) for a detailed description of several experiments and a review of the literature up to 1997.

Milinski placed a predator, a pike, in a closed compartment at one end of a rectangular aquarium. At the other end he released a single prey, a stickleback. The stickleback could see its own image in a mirror. The subjects reacted to their mirror images as if they were conspecifics. In one condition ('cooperating mirror') the mirror was placed parallel to the long side of the aquarium, which gave an individual the impression of a conspecific swimming alongside it as it approached the predator. In a second condition ('defecting mirror') the mirror was put at an angle such that the approaching fish could see a conspecific apparently lagging behind it and eventually disappearing. According to Milinski (1987), the behaviour of the fish corresponded to the IPD as follows. The stickleback approached the pike in a stop-and-go fashion. Each 'go' was counted as a round in the game. The highest payoff in the IPD (T) was assigned to the virtual fish that stayed behind, while a subject that moved closer to the pike was assigned the lowest payoff (S). The second-largest payoff (R) was allocated to an approaching fish with a 'cooperating' mirror and the third-largest payoff (P) to a fish that did not approach (Fig. 2a).

A Critique of the 'Motive 3' Experiments

I discuss these experiments in more detail, because I have strong doubts about their general validity, the interpretation of some results and the implementation of the paradigms tested.

(1) The blue jay experiments are de facto Skinner box tests of instrumental learning in which cooperation played no role. In a commentary on Clements & Stephens (1995), Roberts (1997, page 1361) remarked that: '[the results] can be explained by arguing that the jays preferred to press the key that always gave the higher reward. … The most parsimonious explanation of each jay's behaviour involves no consideration of the behaviour of the other individual'. In other words, the animals, trained to peck the C-key by a process of operant conditioning before the actual experiment, continued to peck the key that usually gave the higher reward, regardless of what their
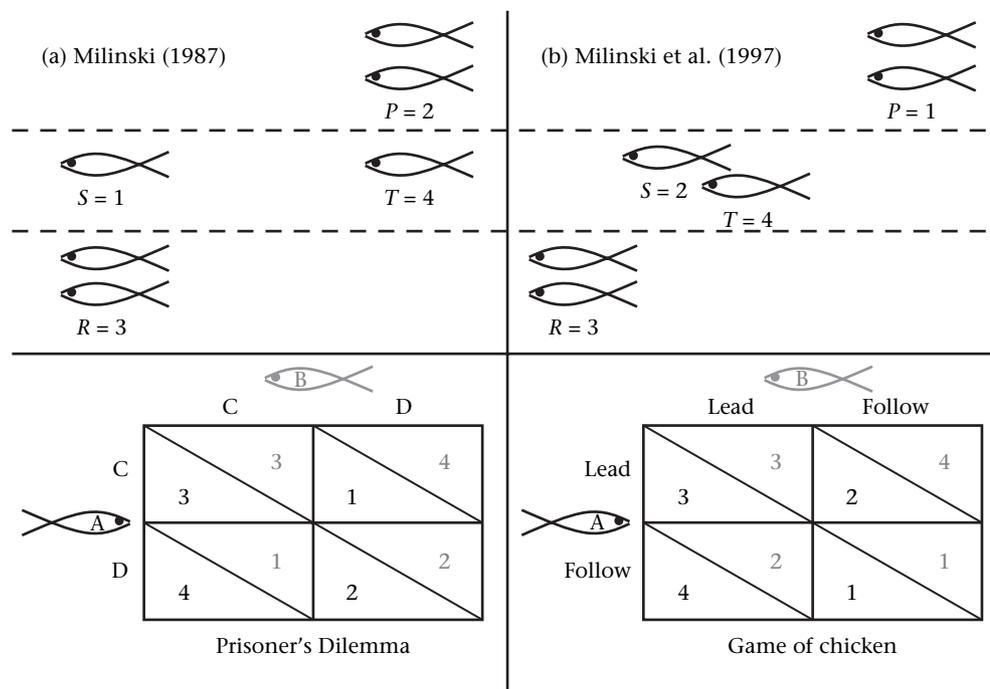
Figure 2. (a) Payoff configuration of the mirror experiment described in Milinski (1987) according to the author (see also Milinski 1990). (b) Reconstruction of the payoff configuration of predator inspection on the basis of information provided by Milinski et al. (1997). The predator is to the left-hand side and the inspecting fish starts from the right in both cases (see text for further explanations).

partner chose. Extinction does not take place if a choice is rewarded often enough. The same argument is also valid for the experiments described by Stephens et al. (2002), who investigated the maintenance, rather than the emergence, of cooperation. The C-perch yielded more than the D-perch during training to make the jays begin with C-choices. This was also true in the test situation, in which the reward accumulated before the bird obtained access, if it continued choosing C. Again, an occasional 'defection' is unlikely to extinguish the response. In the control experiment, each round was rewarded immediately, however, which implies that 'defecting' yielded the highest reward per round. Thus, instrumental conditioning can explain the difference in results for the two conditions (see also the discussion in Hauser et al. 2003). The effect of discounting that was reported is indeed highly interesting, but one does not need two birds acting in parallel to produce this effect (see references in Stephens et al. 2002 and their 'Preliminary Experiment' described in the online material).

Hall (2003) described an experiment with a straightforward Skinner box design in which a single pigeon was confronted with a payoff configuration as in the two-player IPD. The same design had been used earlier by Green et al. (1995). Hall's Skinner box played two strategies RANDOM and TIT-FOR-TAT (TFT). In both cases the pigeon played 'defect' with increasing frequency over the series of trials. Against RANDOM this strategy indeed resulted in an increased reward, but not against TFT. The explanation is that the birds played a short-sighted strategy and reacted with 'defection' (almost) every time they got the 'sucker's payoff' (S), that is, no reward at all. Hall (2003,

pp. 204–205) concluded: 'It, thus, appears that the birds were responding to the local reinforcement contingencies'. This conclusion also fits the blue jay experiments.

The difference between the design of Hall (2003) and the experiment of Stephens et al. (2002) was the presence of the stooge in the latter. But does this constitute an essential difference? There was neither a control experiment without a stooge, nor a procedure to test whether the subjects actually used information obtained from the stooge. In a more recent paper, however, Stevens & Stephens (2004) showed that the choice made by a jay is contingent upon the choice of its partner. The apparatus differed from that described above in that the jays were in chambers facing each other and separated by a transparent partition. Both C-perches were at one side of the apparatus and both D-perches were at the opposite side. Within each 'round' one of the jays could wait for the other to make its choice. The results showed that a choice for the C-perch was more likely after the partner had chosen this perch in either the previous or the same round. However, it remains unclear exactly how the birds used the behaviour of the partner to inform their own choice. A parsimonious explanation is that the second bird chose the perch at the same side of the apparatus as its partner, because the feeding activity of its partner on one side was connected to more food at that side. In nature, foraging in the vicinity of successful conspecifics is a commonly used strategy and usually labelled 'local enhancement' (Thorpe 1956). An obvious control would be to swap the C- and D-perches in one chamber. The 2004 experiment has the flavour of an IPD, but the possibility of

reacting to the partner's choice within the same round removes the dilemma for one of the birds. I return to this point in the next section.

(2) Neither the 2002 blue jay experiment nor the predator inspection experiment meets the requirements of the two-player IPD paradigm. Given that these experiments were designed by researchers who apparently held a strong conviction that the essence of cooperation is captured by the IPD, it is astonishing to see that neither fully complies with the game's rules. It seems unlikely that the jays experienced a payoff configuration as dictated by an IPD design in the experiment described by Stephens et al. (2002). The authors considered each choice as one round of the game in all treatments. From the viewpoint of the jays, however, four hops on a perch led to a single reward in the accumulation treatment. This is, in effect, a 'fixed rate reinforcement schedule'. As Skinner (1938, page 300) noted: 'A group of acts acquires the status of a single response when its reinforcement depends upon the completion of a number of similar acts'. The visible addition of food after each hop is only likely to have served as an additional reinforcer. Thus, one round in the repeated game corresponds to a group of four hops resulting in a single reward rather than one hop.

Many arguments have been put forward against the conclusion that predator inspection resembles the IPD. Most are listed and critically evaluated in Dugatkin (1997, pp. 63–70; see also Stephens et al. 1997). Several arguments against the IPD interpretation remain, however. I realize that adding further words to this drawn-out discussion risks annoying some readers, but I think it is important to look at this case again. For many, the predator inspection experiments remain proof of the success of the IPD paradigm, and thus an argument against one of the main conclusions of this review: namely that communication facilitates cooperation in many cases and is essential to its success in some.

The payoff configuration does not conform to the IPD payoff matrix as originally proposed by Milinski (1987) (Fig. 2a). His translation of behaviour into (relative) payoff was based on several assumptions (see also Milinski 1990). The most important one was that, in a natural context, a fish lagging behind would gain information of similar value as the approaching fish, but without running the same risk (i.e. $T > R$). When neither fish approaches, both get the same low value information (i.e. $P < R < T$). Thus, for T to be considerably greater than P, information needs to be transferred from a fish close to the predator to a fish at a distance. The operation of such a mechanism was suggested by the work of Magurran & Higham (1988) on minnows that witnessed a conspecific being attacked by a model pike, but could not see the pike themselves. The only direct evidence of onlookers changing their behaviour in reaction to an *inspecting* conspecific was reported by Pitcher et al. (1986). Importantly, however, this reaction occurred only *after* the inspectors returned to the shoal and showed a specific behaviour pattern ('skittering'). I am not aware of observations showing that information is transferred to an onlooker from a fish *while approaching a predator*. It is much more likely that information about the predator is privately obtained through chemical signals, which get weaker with distance (Brown & Godin 1999; Brown & Magnavacca 2003).

Does the IPD payoff configuration hold under the assumption that no transfer of information takes place between prey fish? The main advantage of sociality for small fish is no doubt the defence against predators, notably as a result of the dilution effect (Hoare et al. 2004 and references therein). No additional advantage from inspecting, for example in the form of 'attack deterrence' (lowering the chance of being attacked by approaching the predator), has been identified so far (Milinski et al. 1997). This means that cooperation between inspectors reduces to 'shoaling' (Lazarus & Metcalfe 1990; Masters & Waite 1990; Noë 1990; Stephens et al. 1997). However, this shoaling behaviour allows the fish to approach the predator more closely by sharing risk, and thus presumably obtain more information (Milinski et al. 1997). Milinski (1992, page 679) rightfully remarked: 'The safety in numbers hypothesis is not a true alternative to the cooperation hypothesis but is a necessary component of it'. Approaching fish indeed run a higher risk than fish that do not approach and this risk increases monotonically with decreasing distance to the predator (Milinski et al. 1997). Milinski et al. also showed that a slightly lagging fish has a much lower risk of being attacked. It seems reasonable to assume that this risk declines much faster with the distance from the leading fish than does the reduction in the value of the information gained. Taken together the most plausible payoff configuration is the following (Fig. 2b): from low to high payoff: (1) not inspecting at all; (2) inspecting alone; (3) inspecting with a lagging companion; (4) inspecting with a companion at the same distance; (5) inspecting while lagging just behind the leader. Ignoring the option of inspecting alone, this is a 'game of chicken', i.e. $S > P$ instead of $S < P$ as in the PD, that is, it is better to lead than not to inspect at all. (The same payoff configuration is obtained by pooling the two noncooperation payoffs (1) and (2). Behavioural ecologists also know this game as the Hawk–Dove game with V (resource value) $< C$ (cost of escalation).) The game is symmetrical and has two Nash equilibria. As soon as one fish moves forward, the symmetry of the game is broken and the other's best strategy is to follow. The cost of such a first move is likely to be small at a great distance from the predator, making it plausible that some asymmetry in the cost of approaching (e.g. because of a size difference, cf. Walling et al. 2004) can solve the dilemma. This is in agreement with the observation that the same fish tends to lead all the way (Parker & Milinski 1997: note that the latter paper offers a much more complicated way to analyse the inspection game). Interestingly, simulations using a genetic algorithm showed that cooperation by way of 'strategic alternation' in the repeated game of chicken is more stable than cooperation in the IPD (Browning & Colman 2004).

The reader should not conclude that I propose to analyse cooperative predator inspection as an iterated game of chicken, because I also object to portraying a single inspection episode as a repeated game (Milinski

1987, 1990). The assumption that each approach bout within an inspection tour corresponds to a round in the IPD implies that the fish evaluates the situation anew after each short move towards the predator. In the case of the 'defecting mirror' this means, for example, that the behaviour of the virtual companion provides the same cue at the start of the inspection tour as when the inspector is close to the predator. I doubt, however, that an inspecting fish close to a predator will rate a short move of a conspecific lagging way behind as a 'cooperative move', or will even pay attention to a laggard. In the mirror experiment the virtual companion is not even visible from positions close to the predator. In other words, each predator inspection trial reproduces a single choice for 'defection' or 'cooperation', but cannot a priori faithfully reproduce all possible strings of cooperation and defection choices of the IPD.

A repeated game can still be the appropriate paradigm when each inspection tour is seen as a single round. For the use of the IPD this introduces a new problem, however. The movements of the two 'partners' are indeed absolutely simultaneous in the mirror experiment as they should be in a genuine IPD, but real fish will almost never move simultaneously, giving the slower fish the advantage of knowing the option chosen by the other. This is the same problem as mentioned above for the experiment of Stevens & Stephens (2004).

At first sight the choice of a two-player model seems odd, if indeed shoaling is the only cooperative aspect of predator inspection. Why would the fish not increase dilution by inspecting with more conspecifics if the opportunity arises? Milinski (1990) argued that cooperation by players caught in a Prisoner's Dilemma becomes very unstable if there are more than two players involved. He therefore argued that the preference for inspection in pairs supports the two-player IPD interpretation. Such a preference, even if more conspecifics are available, has indeed been shown for some species of small fish (Milinski et al. 1990b; but see Magurran & Pitcher 1987 and Turner & Robinson 1992). This also seems to refute the 'shoaling without information transfer' argument. However, in my eyes, the preference for forming pairs fits perfectly well with it. The strongest gain from dilution is when group size increases from one to two, if we assume that aggregations grow with one individual at a time. The dilution effect becomes stronger still when more individuals are added, but coordination problems also increase (when to start, how fast and how far to move, etc). A group size of two could be the optimal compromise between these two counteracting forces.

A Two-player IPD Experiment is Hard to Design

Apart from the issue of the validity of the theoretical foundations of an experiment, one also has to solve the practical problem of faithfully converting the essentials of the model. I use the design of experiments based on the two-player IPD as an example to point out problems, some of which are general, others specific to the IPD paradigm. The experimenter faces two major challenges: (1) find the right combination of species and apparatus to turn all features of the IPD into reality and (2) prove that the 'players' indeed experience an IPD.

External payoffs

Animals can hardly be expected to abandon their natural behavioural repertoire as superfluous baggage once they enter the experimental apparatus. I pointed out above that 'being with a conspecific' can be a reward in itself. Such 'external payoffs', or 'intrinsic reinforcement' in the jargon of psychology (Schuster & Perelberg 2004), can cause considerable discrepancy between payoffs intended by the experimenters and payoffs as perceived by the subjects. The problem is that it is hard to quantify such payoffs. We often do not even know whether such payoffs are positive or negative. Most species used in cooperation experiments use 'safety-in-numbers' as a defence against predators. Such species remain inclined to seek the vicinity of conspecifics even in a 'safe' cage or aquarium and in the absence of a predator. Masters & Waite (1990), in a predator inspection experiment, showed that it makes little difference whether or not a predatory fish is visible. Seeing a conspecific in an otherwise stressful environment may therefore be a reward in itself (Steer & Cuthill 2003). Gardner et al. (1984) reported that rats cooperated better if they could see each other, a result that was confirmed for capuchin monkeys by Mendres & de Waal (2000). Schuster & Perelberg (2004) gave rats the choice to work together or to work alone for the same quantity of food and thus explicitly showed that rats prefer company. Subjects may also experience the presence of a conspecific as a negative reinforcer, because they see it as a competitor for food, territories or mates.

Information exchange without communication

The hardest problem to overcome for anyone designing an IPD experiment is controlling the flow of information between the players. The IPD paradigm prescribes that no information is received about the choice being made in the same round by the other player. A drastic solution is to block all possible communication during the time in which choices are made. This makes it necessary, however, to prove that the subjects are still aware of each other's presence and of each other's influence on payoffs, and know which choice the partner has made.

Perceiving the other as a partner

The keas of Tebbich et al. (1996) routinely coerced their unwilling partners to 'cooperate'. An adult male chimpanzee, confronted with the same apparatus as used by Chalmeau et al. (1997), did not coerce his juvenile partner, but sometimes carried her towards the levers (Chalmeau 1994), showing that he was aware of her role. These findings, together with the results of Hauser et al. (2003) and Cronin et al. (2005), show that animals can be aware of the fact that the partner is instrumental in obtaining a reward. This makes it all the more difficult to show that such awareness of the partner's role occurs, while simultaneously ensuring that communication is impossible or

meaningless, as the IPD paradigm requires. The failure of primates to follow mentally the invisible displacement of objects (reviewed in Tomasello & Call 1997; Call 2000; Neiworth et al. 2003) suggests that they will also have problems perceiving an individual as a partner after it disappears from sight. In one experiment, Mendres & de Waal (2000) left a small hole in an otherwise opaque separation. For primates that live together this apparently suffices to know who is on the other side. Vocal signals remained possible, however, which would make this a less than ideal solution for an IPD experiment. A threat grunt by a dominant individual could make the subordinate partner aware of the potential punishment that awaits him in the communal cage with dire consequences for the payoff matrix constructed by the experimenter.

The choice of a partner over another individual, or eventually over a machine, would show that the subject is aware of the role the other plays. However, when the choice process itself becomes part of a meta-game, then it is no longer an IPD (cf. Noë 1992).

Information about the choice made by the partner

How does an animal in an IPD experiment obtain information about the choice a partner makes after, but not during, the choice process? I see two mechanisms. (1) Each player infers the choice of the other player on the basis of its own choice and the payoff it receives. This requires considerable cognitive abilities, or a rather fine-tuned selection of conditional strategies combined with payoffs of constant absolute value. This form of inference cannot be made if payoffs vary, as will be the rule rather than the exception in nature. At the very least the subjects should be able to rank four different payoffs in value, that is, reach a minimal level of numerical or ordinal competence, something which is not a self-evident ability of nonhuman players when numbers become higher than five or six and differences are small (Tomasello & Call 1997; Shettleworth 1998; Hauser 2000). (2) Each player is informed about the other's choice after that choice has been made. This could be done, for example, by using delayed video. The need for such methods would also make it painfully clear that the experiment is far removed from mimicking natural cooperation.

The IPD paradigm does not make any assumptions about communication as such, but rather assumes that neither partner has an interest in sending honest signals and, therefore, that signals should be ignored. But how can we tell that animals perceive the situation as one in which the partner has no interest in giving honest signals? The life of most animals is not a string of identical situations and certainly not a string of Prisoner's Dilemmas. Suppose members of species x are also regularly confronted with another game with a slightly different payoff distribution, for example Maynard Smith's (1983) 'synergistic mutualism-game'. This game has two Nash equilibria: 'both cooperate' and 'both defect'. Communication is useful and reliable, because it prevents players from slipping out of the more highly rewarded cooperative equilibrium into the trap of mutual defection. Failure

to recognize the game being played may result in reeling off the wrong strategy, a problem well known for human subjects (Janssen 2003 and references therein).

Animals can in principle perform much better than human players in strategic games and come close to playing strategies that are equivalent to so-called 'super-rational' strategies as long as they perform in conditions to which their strategies are adapted (Hammerstein 2001). The crux is that the experimental game must contain the right cues to trigger the strategy evolved for the equivalent natural situation. It is a priori unlikely that animals have an evolved strategy for situations that are rare or nonexistent in nature.

Conclusion: two-player IPDs are (almost) as rare in the laboratory as in nature

It should be clear that either I am putting up a straw man as far as IPD experiments are concerned or some colleagues are searching in the dark for a cat that is not there. Ultimately the validity of an experiment based on a theoretical model stands or falls with the validity of the model itself. My conclusion is that it is hard to design a valid experimental two-player IPD with animals for the same reasons that make it unlikely that one will find this game in nature. Even territorial neighbours, whom I presented above as players in a naturally occurring iterated two-player game, communicate extensively during their border duels.

In sum, the IPD is hardly relevant as an explanatory model for cooperation in animals, since the hallmarks of animal cooperative behaviour, such as communication, coordination and partner choice, are completely ignored. The two-player IPD is not only a theoretician's toy, however. It retains great value as a benchmark in the study of human behaviour, where one is interested in understanding deviations from rational behaviour (reviewed in Colman 2003; Fehr & Henrich 2003), gender differences (Ortmann & Tichy 1999) and so forth.

GENERAL ISSUES

Instrumental Versus Communicative Cooperation

A dichotomy emerges in the way cooperation is conceived and defined. At one end of the spectrum anything resulting in a net benefit for both subjects is considered cooperation, even if subjects learn to interact with an apparatus or conspecifics by 'trial-and-error'. A central assumption, which follows from the choice of the IPD as paradigm, is that no reliable information is obtained directly from the partner and performance is not improved by communication. This reduces the problem of cooperation to one of making the right connection between cause (the individual's own behaviour) and effect (the economic outcome), which is very similar to solving an optimal foraging problem. This assumption allows the testing of cooperative strategies with a single animal in a Skinner box, as exemplified by the experiments of Hall (2003; see Schuster & Perelberg 2004 for a review of

further examples). A complete experimental representation of cooperation can then be constructed by connecting two such Skinner boxes, as was done by Clements & Stephens (1995) and Stephens et al. (2002). Clements & Stephens (1995, page 53) put it this way: 'We do not suppose that natural selection has favoured cooperative key-pecking in Skinner boxes'. I propose that this should be called 'instrumental cooperation', following Roberts' (1997) suggestion that the behaviour shown in the experiment of Clements & Stephens (1995) is best described as a modification of natural foraging behaviour by instrumental learning.

At the other end of the spectrum attention is paid to behavioural mechanisms that make naturally occurring cooperative interactions work, such as mechanisms that help to initiate cooperative interactions, to assess a partner's behaviour, or to influence that behaviour. An important assumption is that cooperating individuals can improve their benefit by communicating with their partners. I therefore suggest the label 'communicative cooperation'.

Hauser et al. (2003) explicitly differentiated between these two modes of cooperation in their experiments with cottontop tamarins. They distinguished between behaviour elicited by the food rewards as such, which could be interpreted as instrumental learning, and behaviour in reaction to the willingness, or lack thereof, of the partner to produce those food awards.

The difference between instrumental and communicative cooperation runs parallel to the dichotomy between by-product mutualism (West-Eberhard 1975) and 'true' cooperation. It is unlikely that cooperative mechanisms evolved specifically in the context of instrumental cooperation or by-product mutualism. Starting and maintaining genuine cooperative relationships, however, calls for specific skills that are likely to be under selective pressure. This selection can result in the evolution of heritable conditional strategies or of cognitive abilities that allow animals to play such strategies.

To get a feel for the difference, consider the 'cleaning' behaviour of oxpeckers and cleaner wrasses. The cleaner fish mutualism forms a complicated evolutionary puzzle, because most client fish actively choose their cleaners and show specific behaviour to allow the cleaners to do their job (reviewed in Bshary & Noë 2003). The oxpecker–herbivore interactions can be largely understood by considering the birds' foraging strategies on hosts that act as a passive substrate (Mooring & Mundy 1996b). Impala sometimes facilitate the removal of their ticks by lowering their ears (Mooring & Mundy 1996a), but this does not compare to the complex client behaviour reported for fish visiting cleaning stations. Other animals seem annoyed by the oxpeckers' parasitic behaviour (domestic cattle in Africa: Weeks 1999, 2000; black rhinoceros in a zoo exhibit: McElligott et al. 2004).

Mendres & de Waal (2000, page 528) shied away from concluding that coordination resulted from any 'understanding' of the necessity for pulling simultaneously, but hypothesized that the monkeys learned 'the contingency between the co-occurrence of their actions and the reward'. The latter interpretation implies instrumental

('trial-and-error') learning. The contingencies involved seem rather complicated, however. The fact that the capuchins made the connection in these experiments, but not in those of Chalmeau, Visalberghi et al., suggests that they extracted essential information from the partner in the former but not in the latter study. Chalmeau's apparatus might have been too complicated, or might have caused too much delay between behaviour and arrival of the reward, to give the monkeys a chance to learn the connection between the partner's behaviour and the reward. The ability to extract relevant information from conspecifics, which need not imply 'understanding' of the effect of the partner's behaviour, is an example of a trait that potentially evolved specifically in the context of cooperation. It is still conceivable that the connection between signals and cooperative behaviour by conspecifics is learned by trial-and-error only, but if cooperation can improve fitness significantly, a selection for efficient communication to facilitate coordination and cooperation is more likely.

Recollections of the Behaviourist–Ethologist Controversy

An article of faith within the 'behaviourist school' was that one could train an animal to do anything that was within its physical abilities by appropriate reinforcement schedules. McFarland (1999) used the observations of Moore (1973), on pigeons in Skinner boxes, to show that this was fallacious: a pigeon can be taught to peck a key to get either grain or water, but key pecking to obtain grain resembles pecking hard kernels and the pecking movements to get water resemble drinking. He also cited Williams & Williams (1969) to show that pigeons easily learn to peck a key for a food reward, but cannot learn to stop pecking if this results in withholding the food reward. These textbook examples exemplify the fundamental difference between the approach of behaviourists and ethologists: according to the latter one cannot properly understand the behaviour of animals without taking its function in their natural environment into account. In some of the cooperation experiments reviewed above cooperation can take any arbitrary form, and gives me the impression that the ghost of behaviourism still haunts the study of animal behaviour.

Sociality and Tolerance as Forms of Cooperative Behaviour

The interpretation of a number of experiments is dependent on what one considers cooperative behaviour to be. Chalmeau et al. (1997) and Visalberghi et al. (2000) attributed the success of their monkeys to two factors: (1) the inclination of capuchins to manipulate objects very often, making it likely that two individuals handled the levers simultaneously, and (2) the high tolerance of capuchins towards conspecifics. In less tolerant species dominant individuals may monopolize the access to the food-spending machine and so block all opportunities to 'cooperate' (see e.g. Chalmeau 1994 for chimpanzees).

This same argument was used by Petit et al. (1992) to explain why two Tonkean macaques sometimes succeeded in jointly lifting a heavy stone covering a reward, whereas baboons (Fady 1972) and Japanese macaques (Burton 1977) failed in the same task.

'Being tolerant' is a general characteristic that distinguishes Tonkean macaques, and several other monkeys, from other primate species (Thierry 2000). Does this generalized form of tolerance qualify as cooperative behaviour? The answer can be yes, if we consider sociality in general (the tendency to aggregate with conspecifics) as cooperative behaviour. Aggregations can have advantages to all participants, such as the reduction in predation risk. I argued above that sharing the risk is the essence of the cooperation between fish that inspect predators together. Tolerance, in turn, facilitates group living by easing tensions from resource competition. Sociality is, however, better considered as a separate phenomenon, because we otherwise risk making the concept of cooperation so broad that it becomes useless.

This does not apply for 'tolerance' used in a different sense: instances in which members of normally rather 'intolerant' species (sensu Thierry 2000), such as baboons, temporarily accept that subordinate group members share a food source with them (Barrett & Henzi 2001; Barrett et al. 2002). Used in this sense tolerance is not a general attitude of a species, but rather a specific service that can be given or withheld and can be bartered against other commodities. To my mind such tolerance clearly qualifies as a 'cooperative investment'.

Searching for Suitable Paradigms

Paradigms based on repeated games can be very useful to guide the study of cooperation, and thus inspire the design of cooperation experiments, but it is a mistake to limit the choice to the two-player IPD and its derivatives. It may prove more fruitful to base experiments on alternative paradigms with the following characteristics: (1) communication should be an intrinsic element; (2) a trial in the experiment, corresponding to a round in the repeated game, should allow the subjects to complete a full 'natural' behavioural sequence; (3) the option of partner choice and partner switching should be given; and (4) attempts should be made to quantify all investments and returns.

The experiments described above and observations of cooperating animals in natural settings give plenty of reason to think that communication plays a central role. I return once more to cooperatively hunting lionesses. During the hunt itself the lionesses can monitor each other's contribution constantly (Stander 1992). Afterwards the spoils have to be split, which is a problem of conflict resolution rather than cooperation, but the problem is rather similar. Communication plays a major role: one takes a bite too much, the other growls in threat, and so on. Connor (1992, 1995b) called this 'parcelling' and presented it as a way of reducing the costs of being cheated in cooperative interactions. This is certainly a valuable approach, but I think the role of communication should

be stressed more. Not only are individual bites small relative to the whole zebra, giving them the character of signals of intention, but they are also embedded in a wealth of further signals such as growls, movements, facial expressions and whipping tails.

The next issue is to decide what unit of analysis is equivalent to a single round of a repeated game? For the lionesses, I see the complete hunt, including the division of the prey, as a single round in a repeated game of many hunts. We have seen that the definition of what counts as a round in the game makes a crucial difference in the experiment of Stephens et al. (2002; see also Mesterton-Gibbons & Adams 2002).

In nature few animals have only a single potential partner or pair up randomly to cooperate. The preference for specific partners as seen in some predator inspection studies, be it on the basis of previous experience with that partner (Milinski et al. 1990a; Dugatkin & Alfieri 1991) or on the basis of size (Walling et al. 2004), adds an argument for the use of partner choice models rather than partner control models. Ideally then, partner choice should be made an explicit option in experiments, with the proviso that one verifies that the subjects actually experience the set-up as a choice between potential partners. Imagine a subject that must choose between two partners, which, because of differences in their behaviour, cause two food dispensers to produce different quantities of food. Preference for the partner associated with the higher quantity of food reveals nothing relevant to the evolution of cooperation, since a preference for richer patches is in the foraging repertoire of most species. The critical observation is how the behaviour of the chosen parties changes towards the choosing animal. They may, for example, yield more to the chooser in an attempt to outcompete each other for the chooser's attention (Noë 2001) or harass the chooser more in the triadic situation than in dyadic interactions with the chooser. The experimental design could be based on almost any of the dyadic cooperation experiments presented above by adding a third individual, so at least one subject has a choice between two partners. For example, de Waal (2000) described a test in which two individuals in adjacent cages alternately receive a bowl of food to see whether they share food by dropping it near the mesh partition. It would be interesting to put three individuals in a row of three adjacent cages and alternate trials in which the individuals on the ends receive a bowl of food with trials in which only the individual in the middle receives food. I would predict that, given enough trials, the amount of food the subject in the middle receives *per partner* increases compared to dyadic trials with the same individuals.

Results of published studies can also be verified in this way. Take, for example, the experiment described by Hauser et al. (2003). Let us say that the two exterior individuals can each simultaneously pull an L-shaped tool. By pulling, individual X obtains one piece of food and M, the individual in the middle, receives two pieces. Individual Y, at the other end, can also give M two pieces, but receives none itself. In the next round, M can give two pieces to either X or Y, receiving none itself. On the basis of the published results one would expect M to give to Y (the 'altruist') rather than to X.

GENERAL CONCLUSIONS

(1) Confusing terminology used in publications on co-operation hinders the exchange of ideas between disciplines. Some of this is due to semantic differences, some to fundamentally different perceptions of what co-operation is and how it should be defined. Choices have to be made between form and outcome and between co-operative interactions and the individual contributions to such interactions. I propose to base definitions on the form of individual strategies and to use only three concepts to describe the core of the matter: cooperation, co-operative investment and cooperative returns.

(2) Some experiments lack virtually all elements that make cooperation such an exciting topic and evolutionary enigma, for example the formation of cooperative partnerships, conflicts over the division of investments and returns, effects on other aspects of long-term relationships, the communication between partners and between partners and bystanders.

(3) The rationale of several experiments based on the two-player IPD game can be called into question, because (1) they do not conform to this paradigm, (2) it is extremely difficult, if not impossible, to translate faithfully the paradigm into an experiment, and (3) the relevance of the paradigm itself is questionable.

(4) There is a gaping chasm between cooperation experiments in which animals de facto interact with a machine and experiments in which animals adjust their actions depending on information received from a conspecific.

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