

Review

Integrating cooperative breeding into theoretical concepts of cooperation

Ralph Bergmüller^{a,*}, Rufus A. Johnstone^b, Andrew F. Russell^c, Redouan Bshary^a

^a Department of Eco-Ethology, Institute of Biology, University of Neuchâtel, Rue Emile Argand 11, CH-2009 Neuchâtel, Switzerland

^b Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

^c Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Received 30 October 2006; accepted 16 November 2006

Abstract

In cooperative breeding systems, some individuals help to raise offspring that are not their own. While early explanations for such altruistic behaviour were predominantly based on kin selection, recent evidence suggests that direct benefits may be important in the maintenance of cooperation. To date, however, discussions of cooperative breeding have made little reference to more general theories of cooperation between unrelated individuals (while these theories rarely address cooperative breeding). Here, we attempt to integrate the two fields. We identify four key questions that can be used to categorise different mechanisms for the maintenance of cooperative behaviour: (1) whether or not individuals invest in others; (2) whether or not this initial investment elicits a return investment by the beneficiary; (3) whether the interaction is direct, i.e. between two partners, or indirect (involving third parties) and (4) whether only actions that increase the fitness of the partner or also fitness reducing actions (punishment) are involved in the interaction. Asking these questions with regards to concepts in the literature on cooperative breeding, we found that (a) it is often straightforward to relate these concepts to general mechanisms of cooperation, but that (b) a single term (such as ‘pay-to-stay’, ‘group augmentation’ or ‘prestige’) may sometimes subsume two or more distinct mechanisms, and that (c) at least some mechanisms that are thought to be important in cooperative breeding systems have remained largely unexplored in the theoretical literature on the evolution of cooperation. Future theoretical models should incorporate asymmetries in power and pay off structure caused for instance by dominance hierarchies or partner choice, and the use of N-player games. The key challenges for both theoreticians and empiricists will be to integrate the hitherto disparate fields and to disentangle the parallel effects of kin and non-kin based mechanisms of cooperation.

© 2007 Published by Elsevier B.V.

Keywords: Cooperative breeding; Evolution; Altruistic behaviour; Reciprocity; Pay-to-stay; Group augmentation; Prestige

Contents

1. Introduction	62
2. Cooperation	63
2.1. Cooperation and the problem of outside options	64
3. Concepts of cooperation and building blocks	64
3.1. Investment (a costly act)	65
3.2. Return investment (a costly response)	65
3.3. Direct or indirect interactions	66
3.4. Positive or negative control mechanism	66
4. Categorising theories of cooperative breeding	66
4.1. Pay-to-stay	66
4.2. Group augmentation	66
4.3. Prestige	67
5. Discussion	67
5.1. How to study cooperative behaviour in cooperative breeders?	68
5.2. New avenues for theoretical research	68

* Corresponding author.

E-mail address: ralph.bergmueller@unine.ch (R. Bergmüller).

5.3.	N-player cooperation	68
5.4.	Outside options: biological market theory	69
5.5.	Symmetric or asymmetric relationships and interactions	69
5.6.	Interactions of kin based and non-kin based cooperation	69
5.7.	Kinship, interdependence and the value of lasting associations	70
6.	Conclusions	70
	Acknowledgements	70
	References	70

1. Introduction

The theory of evolution by Natural Selection appears at first glance to predict that individuals will be selfish rather than cooperative (Darwin, 1859; Fisher, 1930). Despite this, cooperation is common throughout the animal kingdom and occurs both between conspecifics and between heterospecifics. A particularly striking example is cooperative breeding, in which individuals help to raise offspring that are not their own (Cockburn, 1998). These ‘helpers’ often (but not always) delay dispersal, engage in various helping tasks and usually reproduce below their potential compared to when breeding independently. Few examples of cooperation can rival the behaviour of sterile workers in eusocial insects, which completely forego the chance to reproduce and often commit suicide in their quest to protect the offspring produced by breeders. However, cooperative breeding is not confined to insects and occurs in several vertebrate taxa, including fishes (e.g. cichlids), birds (e.g. corvids and many passerines in Australia) and mammals (e.g. canids, viverrids, humans). Although helping in provisioning the young has received the majority of interest, helpers can also care by ‘nest’ building, tending of eggs or young, allo-suckling, as well as carrying, huddling and defending (Cockburn, 1998; Dickinson and Hatchwell, 2004; Russell, 2004).

The theory of inclusive fitness (Hamilton, 1963, 1964) showed that cooperative breeding could (at least in principle) be explained within the framework of natural selection acting on individuals, by invoking indirect fitness benefits from helping closely related kin. Kin selection remained the main theoretical explanation for cooperative breeding for a long time (but see Gaston, 1978; Brown, 1987) since, in addition to the compelling logic of kin selection theory, empirical studies revealed that most helpers are related to the breeders whom they assist (Emlen, 1997; Dickinson and Hatchwell, 2004). Because kin selection was supposed to select against ‘cheating’, empiricists turned away from questions concerning the evolutionary stability of cooperative behaviour (how and why ‘cheats’ that refrain from help might be ‘punished’), and focussed instead on the observable consequences of helping behaviour. Only in recent years scientists have started to question whether kin selection alone is sufficient to explain cooperative behaviour in cooperative breeding, in particular among vertebrates (Cockburn, 1998; Heinsohn and Legge, 1999; Clutton-Brock, 2002; Ridley and Sutherland, 2002; West et al., 2002b). For instance, it has been argued that indirect fitness benefits due to helping are rarely high enough to compensate for not breeding independently (Dickinson and Hatchwell, 2004), and competition between

relatives may counterbalance and even outweigh kin benefits (West et al., 2002b). Also, it is now apparent that helpers in cooperative breeding systems are commonly less related to the breeders than has been generally assumed (Cockburn, 1998; Clutton-Brock, 2002). While helpers doubtlessly make recognition errors, these are unable to account for all instances of cooperation between non-kin. Therefore, although the majority of cooperative breeding systems involve some degree of kinship (Emlen, 1995), this may often be due to the benefits of philopatry and helping rather than the benefits of helping relatives *per se* (Clutton-Brock, 2002).

For the above reasons, possible direct benefits of helping have become the focus of greater interest (Gaston, 1978; Brown, 1987; Clutton-Brock and Parker, 1995; Cockburn, 1998; Clutton-Brock, 2002; Kokko et al., 2002; Bergmüller et al., 2005b; Bergmüller and Taborsky, 2005; Komdeur, 2006). There is consensus that a key factor explaining why helpers delay dispersal is ecological constraints, which limit the chances to survive or breed independently (Brockmann, 1997; Hatchwell and Komdeur, 2000). Hence, although helpers would do better if they were to succeed in breeding independently, they choose a ‘best of a bad job’ strategy and stay, either to queue for the breeding position or to wait until the chances of breeding independently have increased (Hatchwell and Komdeur, 2000). However, to explain why helpers stay is not to solve the question of why helpers engage in helping, because species exist in which individuals stay but do not help, and others in which they help but do not stay (Cockburn, 1998; Russell, 2004). Likewise, to explain why helpers stay is not to explain why helpers reproduce below their potential, since the degree of reproductive skew varies widely within and between species (Magrath et al., 2004; Russell, 2004). While there are a few apparent exceptions (e.g., Emlen and Wrege, 1988; Russell and Hatchwell, 2001), to understand cooperative behaviour in cooperatively breeding species it is generally necessary to consider the combined influences of direct and indirect fitness benefits and their interactions. However, for our present purpose, explanations of cooperative breeding based on direct fitness benefits are our main interest, because of parallels that may be drawn between these concepts and more general theories of cooperation. Below we briefly summarise three popular concepts that invoke direct benefits to account for helping behaviour: pay-to-stay, group augmentation, and prestige.

The pay-to-stay hypothesis proposes that help provided by helpers can be viewed as a form of ‘rent’ paid to dominants in return for being allowed to stay in their territory (Gaston, 1978). If helpers do not provide sufficient help, the dominants

should punish helpers (i.e. impose costs) by (a) reinforcing or encouraging helping or (b) by evicting them from their territory. Evidence for pay-to-stay has been scarce (Reeve, 1992; Mulder and Langmore, 1993) but has recently begun to accumulate in a cooperatively breeding cichlid *Neolamprologus pulcher* (Balshine-Earn et al., 1998; Bergmüller et al., 2005b; Bergmüller and Taborsky, 2005; Stiver et al., 2005).

The group augmentation hypothesis suggests that individuals survive or reproduce better in large groups. Hence, individuals benefit from helping to increase group size, e.g. by caring for offspring of others even if they are unrelated or by recruiting new group members (Woolfenden, 1975; Brown, 1987; Kokko et al., 2001). Benefits arising from group augmentation can be passive (without investment (i.e. a costly behaviour)), group members automatically share benefits (Clutton-Brock, 2002) if the mere presence of individuals provides by-product benefits to other group members, e.g. due to safety in numbers effects. Alternatively, in active group augmentation investments are involved, e.g. helpers may assist breeders because the offspring they help to raise will later help them. One example of passive group augmentation may be provided by a cooperatively breeding cichlid, where large groups were more stable between years (Heg et al., 2005). Also, territories of large groups have been found to be more densely occupied (less shelters available per helper) than territories of small groups. This suggests group augmentation benefits may reduce the need for shelter for each helper and also may compensate for increased competition in more densely occupied territories (Bergmüller et al., 2005a). However, conclusive evidence, particularly on the existence of active group augmentation, is currently lacking.

The prestige hypothesis proposes that helping behaviour may be used as a signal of quality. By helping, helpers thus gain social prestige which may increase the chances of finding a mate or, more generally, a cooperation partner (Zahavi, 1995). For instance, in Arabian babblers (*Turdoides squamiceps*) individuals sometimes reject help they are offered and helpers were observed to compete over opportunities to behave altruistically (Carlisle and Zahavi, 1986). This possibility was treated more generally with the concept of ‘competitive altruism’ (Roberts, 1998): when there is variation between individuals in the tendency or capability to act cooperatively and individuals can choose between partners, individuals may compete for partners by being cooperative.

These direct mechanisms to explain helping in cooperative breeders were developed without explicit links to existing, supposedly more general theories of cooperation between unrelated individuals (Cahan et al., 2002). As a consequence, the terminology used in the two fields differs and we believe that this is hindering a fruitful exchange of ideas. As it stands, cooperative breeding has received little attention from theoreticians interested in the general issue of cooperation among non-relatives, while those interested in cooperative breeding have seldom drawn on general theories from the literature on the evolution of cooperation.

The aim of this paper is to bridge the gap between theories of cooperation and of cooperative breeding, and to stimulate greater cross-disciplinary research between these fields. We suggest to

theorists in cooperation research that the scope for testing their ideas in cooperative breeding species is immense, and to empiricists studying cooperative breeding that ideas from cooperation theory can readily be applied to their study systems, with fruitful results. Finally, we show that some phenomena found in cooperative breeding species are not fully captured by existing game theoretic models. However, all mechanisms can be formalised in game theoretical terms, which should fuel the development of more comprehensive models in cooperation theory. Our examples are biased towards vertebrate systems, for kin selection is still the dominant theory in explaining cooperative breeding in invertebrates (Foster et al., 2006), but see (Wilson, 2005; Wilson and Hölldobler, 2005). Nevertheless, since cooperative breeding is a continuum (Sherman et al., 1995), much of our paper is relevant to those interested in social invertebrates.

In Section 1, we provide definitions of some key terms relevant to cooperation. In Section 2, we introduce four key questions that can be used to categorise a wide range of theories of cooperation. In Section 3, we apply these questions to the concepts of pay-to-stay, group augmentation, and social prestige that were introduced above. Finally, in Section 4 we suggest promising issues for future research that attempt to integrate studies of cooperative breeding into more general discussions of the evolution of cooperation.

2. Cooperation

The terms cooperation, mutualism, cooperative behaviour and altruism are often used interchangeably, which has led to confusion and hinders discussions about the issues concerned (Bshary and Bronstein, 2004; Noë, 2006). While we cannot resolve this issue here, we ourselves will distinguish between them, and we therefore begin by explaining our usage. The key distinction we wish to make is between cooperation (an interaction between two or more individuals) and cooperative behaviour (an action or actions taken by a single individual). In this review we will focus on the factors that account for the maintenance of cooperative behaviours in cooperatively breeding species.

We define cooperation as an interaction between individuals that results in net benefits for all of the individuals involved. Parasitism is defined as an interaction that yields a net benefit for one individual but a net cost for other(s), and competition as an interaction that entails net costs for all players. Following traditional terminology (Bronstein, 2001), cooperation refers only to intraspecific interactions; we use the term mutualism to refer to equivalent interspecific interactions. However, we will make an exception by using the term ‘by-product mutualism’ in intra-specific interactions because it is an established and widely used term. In studies of cooperative breeding, researchers have focussed mainly on the outcomes of helping. For example, they have asked whether helpers confer a net fitness benefit on breeders, comparing the number of offspring raised with or without helpers. In our terms, they are attempting to determine whether cooperative breeding is indeed a form of cooperation.

In general cooperation theory, researchers are more concerned about explaining cooperative behaviour, which we define as an act performed by one individual that increases the fitness

of another. Turning to the fitness consequences of such an act for the actor (rather than for the recipient), cooperative behaviour can be obviously self-serving (Cant and Johnstone, 2006), if it entails an immediate increase in the fitness of the actor (irrespective of the partner's subsequent behaviour); alternatively, it can be seemingly altruistic, if it entails at least a temporary reduction in the fitness of the actor (irrespective of the partner's subsequent behaviour), as in the well-known prisoner's dilemma game. In the latter case, we say that the actor invests in another individual. Any kind of investment is interesting from an adaptive perspective, as one must ask what selective factors prevent individuals from withholding their investment and thereby escaping the fitness cost that it entails.

The term investment applies not only to cooperative behaviour in a prisoner's dilemma, but also to the many instances in nature in which there is a continuum of possible investments in a partner (e.g. nectar production, time spent vigilant, food provided to third party offspring). We have to explain the existence and maintenance of any form of investment, independently of whether the benefits of this investment are accrued immediately, with delay or apparently never (as in the case of kin selected investment in which benefits are due to indirect fitness gains). Ultimately, evolutionary theory predicts that any investment is likely to prove only *apparently altruistic* and will be explained by hidden benefits, e.g. due to kin selection or later reciprocation (Trivers, 1971).

The distinction between cooperative interactions and cooperative behaviours/acts is important, because cooperative breeding may well involve many cooperative acts, yet at the same time may qualify as parasitism in terms of its net outcome. For instance, helpers may perform a cooperative act in providing a breeder's offspring with food, yet the presence of a helper may nevertheless impose an overall net cost on the breeder.

2.1. Cooperation and the problem of outside options

The net cost or benefit of an action must always be defined relative to some alternative behavioural option. For instance, in the case of cooperative hunting, an individual may stand to gain more by hunting with individual A than by hunting alone, but it may stand to gain less than by hunting with individual B. Since benefits or costs are defined relative to specified alternatives, one has to determine and refer to these 'outside options'. Partner choice is a key component of cooperative interactions (Bshary and Noë, 2003) and biological market theory (Noë and Hammerstein, 1995; Noë, 2001) explores precisely such effects of partner choice when trying to understand shifts in investments or pay off distributions between partners. Hence, a key challenge for both theoreticians and empiricists will be to determine the alternatives available to individuals compared to what they actually do. In this respect, a useful definition of cooperative behaviour is: an individual behaves cooperatively if the resulting payoff for its partner is higher than the average payoff for the relevant type of interaction (Bull and Rice, 1991). According to this definition, even parasites can behave cooperatively if they exploit their host less than do their conspecifics, even though the outcome would still be called parasitism.

3. Concepts of cooperation and building blocks

Cooperation theory has suggested a large number of mechanisms that might potentially maintain cooperative behaviour between unrelated individuals, applicable to both intraspecific cooperation and interspecific mutualism (Connor, 1995a,b; Dugatkin, 1997; Bergstrom et al., 2003). To name concepts we consider relevant for cooperative breeders (described in Box 1), cooperative behaviour may be due to by-product mutualism, pseudo-reciprocity, negative pseudo-reciprocity (i.e. sanctions),

Box 1.

By-product mutualism results when individuals generate benefits to others as a by-product of performing a self-serving act (West-Eberhard, 1975; Brown, 1983). For example, if two golden jackals hunting the same prey together are more successful than each individual hunting alone, cooperative hunting results in by-product benefits for both (Lamprecht, 1978). Note, however, that when the benefits resulting from cooperative hunting are due to coordinated behaviour, the coordination itself can be an investment, and the contribution to coordination by each partner needs to be explained (Noë, 2006). **Pseudo-reciprocity** prevails when an individual performs an investment that promotes the self-serving behaviour on the part of the receiver which in turn benefits the investor as a by-product (Connor, 1995a; Leimar and Connor, 2003). An example is ants tending mushroom cultures (Mueller et al., 1998). Ants benefit by improving self-serving growth of the mushrooms when they later harvest some of the mushrooms. In **negative pseudo-reciprocity** (also termed 'sanctions' in the ecological literature (West et al., 2002a)), an individual terminates an interaction to avoid immediate fitness losses if the partner does not invest (or overexploits) thereby stabilising future benefits. Yucca trees, for instance, may selectively abort fruits that contain too many larvae of its pollinator moth as the larvae would eat too many seeds (Pellmyr and Huth, 1994). In **positive reciprocity** individuals exchange investments, such that the costs of the investments they make are outweighed by the benefits they receive in return. 'Reciprocal altruism' (Trivers, 1971) applies when individuals alternately take the role of the 'altruist' and the beneficiary, while 'simultaneous altruism' has been formalised in the iterated prisoner's dilemma (IPD, Axelrod and Hamilton, 1981). A key issue is that individuals willing to cooperate must be able to control the behaviour of their partner to avoid being exploited by self-serving individuals. While the IPD has been

Box 1 (Continued)

popular among theoreticians for a long time, its usefulness appears to be limited as there are still remarkably few empirical examples (summarized by Dugatkin, 1997) and several assumptions made by the IPD regarding game structures are violated in most real life interactions (Roberts, 1998; Hammerstein, 2003; Bshary and Bronstein, 2004; Noë, 2006). In contrast, parcelling an interaction into several small cooperation bouts (Connor, 1995a) may solve the problem of cheating in reciprocal interactions in a more simple way because it automatically secures further receiving. The key point is that at each moment of decision, cheating is an unprofitable option because the relatively small benefit of cheating (receiving a small free benefit) is outweighed by the consequences of terminating the interaction (a loss of many small future benefits). Reciprocal grooming in impalas (Hart et al., 1992) may be a good example of parcelling. **Negative reciprocity** promotes investment by an actor who thereby avoids a negative response (punishment) to any failure to invest (cheating) (Clutton-Brock and Parker, 1995). For instance a cleaner fish that cheats a resident client fish by biting it to get the more preferred mucus rather than merely removing parasites will sometimes be chased by the victim. Subsequently, the punished cleaner will give this client a particularly good service during the next interaction (Bshary and Grutter, 2002b; Bshary and Grutter, 2005). In contrast to reciprocal altruism in which the exchange of beneficial acts maintains cooperation, cooperative behaviour resulting from punishment depends on threat. Therefore, single acts of punishment combined with communication (i.e. signalling of threat) may promote long-term cooperative behaviour even if reinforcement only takes place infrequently (Bergmüller and Taborsky, 2005). In **indirect reciprocity** based on image scoring (Alexander, 1987; Nowak and Sigmund, 1998), individuals invest because this increases the probability that observers will invest in them in the future. Investment thus is a consequence of the increase in image or reputation in the original investor. Currently, there is evidence only in humans for this particular explanation of cooperative behaviour (Wedekind and Milinski, 2000). In theory, also **negative indirect reciprocity** based on image scoring due to seemingly spiteful behaviour towards others may promote cooperative behaviour because it discourages observers from acting non-cooperatively towards the perpetrator (Johnstone and Bshary, 2004).

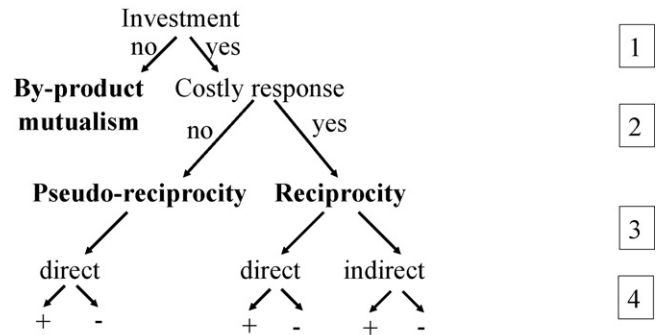


Fig. 1. Hierarchical classification of mechanisms that can maintain cooperative behaviour. By-product mutualism does not involve [1] investments that are directed towards others. An investment may be performed to obtain benefits resulting from the self-serving behaviour of the receiver (i.e. pseudo-reciprocity), without eliciting return investment. Alternatively, an investment may be [2] made in expectation of an investment in return, resulting in reciprocity. The investor may obtain benefits [3] either directly or indirectly (i.e. via third parties). [4] Cooperative behaviour may be stabilised by costly acts or by-products resulting from self-serving responses by the receiver (or third parties) that have either positive (+) or negative (–) effects on the partner.

positive reciprocity, negative reciprocity (i.e. punishment) or indirect reciprocity.

At first sight, this plethora of concepts seems confusing. However, we will show that all can simply be categorised by asking four key questions. We are fully aware that our approach represents a simplification. Further questions could be asked and a more detailed classification developed (e.g. Bshary and Bronstein, 2004). We will address some of these additional issues in the discussion. Here, however, we develop a simple, hierarchical classification of explanations for cooperative behaviour based on our four key questions (Fig. 1). (1) The first question to ask is whether or not an individual invests in a partner. (2) Second, if investment by one or both partners occurs, one has to ask whether the investment elicits a return investment or not. (3) Third, the returns on an investment may be provided directly by the beneficiary or indirectly via third parties. (4) Fourth, cooperative behaviour may be stabilised due to positive or negative effects of an individual on a partner.

3.1. Investment (a costly act)

Like previous authors, we define an investment as a costly behaviour which benefits others (Connor, 1995b; Bshary and Bronstein, 2004). An investment in this sense is synonymous with a temporarily altruistic act. We add to this definition that investments are made in ‘expectation’ of a return, that is, each investment is ultimately performed to promote own interests. A cooperative interaction without investments towards other individuals involved is called by-product mutualism.

3.2. Return investment (a costly response)

In general, investments promote own interests by altering the behaviour of the receiver. An individual may invest (a) to gain access to predictable benefits (assured returns) or (b) in ‘expectation’ of an investment in return. (a) In pseudo-reciprocity an

investment results in predictable benefits because it enhances the by-product benefits that accrue due to the self-serving behaviour of the receiver (not a return investment). Note, that at least in theory (we do not know of any example) both partners may independently invest into the partner to gain by-product returns (2-way pseudo-reciprocity, Leimar and Connor, 2003), which would be difficult to distinguish from true reciprocity in practice. (b) In reciprocity, an investment is favoured due to the costly response (return investment) of the receiver. An investment of this kind does not lead to predictable benefits because the receiver also has the option of whether or not to invest in a response. Hence, the risk of cheating arises and furthermore the possibility for negotiations and regulation of investments based on the expected benefit.

3.3. Direct or indirect interactions

Interactions are direct if the beneficial returns of an investment are due to the response of the recipient, as for instance in reciprocal altruism (Trivers, 1971). Alternatively, an interaction is termed ‘indirect’ if an individual A that helps B will gain from an investment made by a third party C, e.g. as is the case in indirect reciprocity based on image scoring.

3.4. Positive or negative control mechanism

If an individual (or a third party) responds to an investment by increasing the fitness of the investor (either through a by-product or through a return investment), the stability of cooperative behaviour is based on reward. We call this a ‘positive control mechanism’. If instead an individual decreases the fitness of a partner (either through a by-product or through punishment), thereby avoiding further fitness reducing acts by a partner, we use the term ‘negative control mechanism’.

In negative pseudo-reciprocity an individual reduces the fitness of a partner as a by-product of a self-serving act thereby avoiding further fitness losses. In contrast, in negative reciprocity punishment is a costly response to cheating and these costs have to be compensated by *future benefits*.

In the next major part of this paper, we will apply the parameter tree (Fig. 1) to evaluate what kind of mechanisms may promote cooperative behaviour in cooperative breeding. As we shall see, some hitherto unexplored parameter combinations may be of major interest to understand cooperative breeding.

4. Categorising theories of cooperative breeding

We focus on three explanations that have been put forward to explain investments by helpers in addition to kin selection arguments: pay-to-stay, group augmentation and social prestige. We will classify these concepts according to the scheme introduced above.

4.1. Pay-to-stay

Consider a subordinate that imposes some cost on an unrelated breeder by remaining in the breeder’s territory. The breeder

may tolerate the presence of the helper in its territory (an investment) in expectation that the helper will help. If the helper reduces or stops helping, the dominant will punish the helper. In response, the helper performs an investment in expectation that this will avoid future punishment (Bergmüller and Taborsky, 2005). This is therefore an instance of *negative reciprocity*. If a helper does not help, the dominant may increase punishment which eventually may lead to expulsion. Interestingly, when punishment actually involves the threat of expulsion the cooperation mechanism may shift from negative reciprocity to *negative pseudo-reciprocity*. This is because under these circumstances, the dominant invests effort in expelling the helper in order to obtain the by-product benefit of terminating the costs that the latter would otherwise impose by its presence. However, it is noteworthy that cooperative behaviour due to negative pseudo-reciprocity or negative reciprocity is based on threat. Cooperation prevails as long as the net outcome remains beneficial for both parties. However, frequent punishment may shift the interaction towards parasitism or competition.

4.2. Group augmentation

Group augmentation may involve a number of mechanisms of cooperation, which can be difficult to separate in practise:

- (1) *By-product mutualism*: In ‘passive’ group augmentation individuals profit from by-product benefits conferred by the mere presence of other group members. As this involves no investments between group members it constitutes a by-product mutualism. For example, helpers may contribute to territory defence because of direct self-serving benefits (e.g. to reduce own predation risk), but their behaviour may benefit others as a by-product.
- (2) *Pseudo-reciprocity*: In ‘active’ group augmentation an unrelated subordinate may provision offspring because the survival of those young provides by-product benefits to the helper, as a result of the increase in group size. In this case the helper clearly invests in the offspring. The offspring will make use of this investment in a self-serving way, i.e. grow and increase own survival. In turn, the self-serving survival of the offspring increases the fitness of the helper as a by-product, e.g. due to reduced risk of predation (Heg et al., 2004).
- (3) *Indirect reciprocity without image scoring*: Individuals (currently helpers) may help to recruit new group members who will later actively help them to raise their offspring, resulting in cross generational reciprocation (also ‘delayed reciprocity’ (Ligon and Ligon, 1978; Wiley and Rabenold, 1984); ‘generational mutualism’ (Brown, 1987)). In this scenario helpers providing food for young will later become indirect receivers of help when they are breeders themselves. According to the decision tree, a helper invests (increases the survival of young) in expectation that the recipient will later indirectly invest in return (costly response) by helping to raise the former helper’s offspring later. No image scoring is involved: boosting the survival of young simply increases the probability that they will be present to

feed the actor’s offspring (in expectation, in turn, that their own offspring will benefit from the subsequent presence of the actor’s young). Interestingly, as each decision to invest is based on the expectation of future benefits, there is no threat of being cheated: a helper that does not help to raise offspring will have less helpers available to help to raise its own offspring. This explanation for helping relies on helpers being able to gain a breeding position in the same group in which they help.

4.3. Prestige

Zahavi (1995) suggested that Arabian babbler helpers compete among each other to assist breeders’ offspring in order to advertise their genetic quality and thereby gain social prestige.

Prestige and image scoring differ in that the former was proposed as a signal of individual genetic quality (a handicap), whereas image scoring is based only on an individual’s past cooperative behaviours towards third parties and assumes no variation in quality between individuals (Lotem et al., 2003). In both cases helping behaviour translates into a gain in reputation that serves to obtain benefits from third parties. Therefore, as regards the signalling effect of helping, prestige and indirect reciprocity based on image scoring are equivalent (Zahavi, 1995; Roberts, 1998; Lotem et al., 2003). However, with regards to the mechanism of cooperation involved, the crucial question to ask is whether the actor benefits as a result of (a) self-serving behaviour or (b) investment by observers.

- (a) A female may choose a helper as a mate because the fact that it helps is a signal of quality that will translate into superior offspring. As a female has a self-serving interest in obtaining a high-quality mate, a helper invests in caring for young to indirectly obtain the by-product benefits resulting from the self-serving behaviour of the female. This constitutes *indirect pseudo-reciprocity*.
- (b) Reputation may, on the other hand, serve to elicit costly help or tolerance from dominants, which stand to gain by encouraging further helping. In this case, helping the young of others can be an investment in expectation of indirect investment in return due to a gain in reputation. For example, breeders may allow or tolerate direct reproduction by a helper that has a reputation for helping. This constitutes *indirect reciprocity based on image scoring* (Lotem et al., 2003).

Below we summarize the connections between concepts in cooperative breeding and cooperation theory (Fig. 2). Based on the above analysis we need to extend the simple decision tree presented before. Also, the concepts we have reviewed include mechanisms that have not yet been explored in general models for the evolution of cooperation.

5. Discussion

Categorising mechanisms for the maintenance of cooperative behaviour by means of a decision tree, we have emphasised

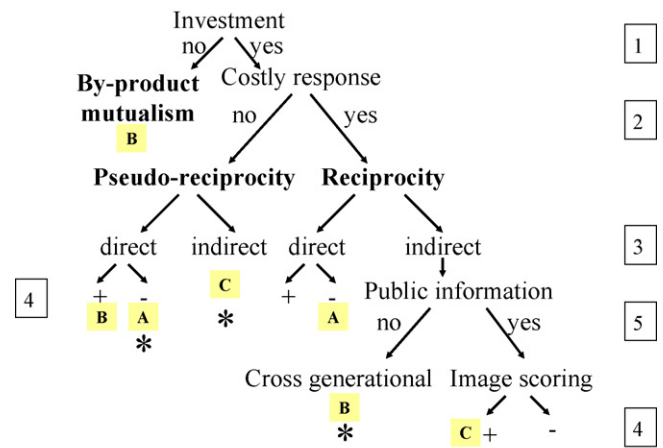


Fig. 2. (A) pay-to-stay corresponds to negative reciprocity (reinforcement) and negative pseudo-reciprocity (helper expelled), (B) group augmentation potentially involves a number of mechanisms (by-product mutualism, pseudo-reciprocity, indirect reciprocity without image scoring (cross-generational)), and (C) prestige corresponds to indirect pseudo-reciprocity or indirect reciprocity with image scoring. In addition to the four questions introduced previously (see Fig. 1), we need to ask an additional question to distinguish between two types of indirect reciprocity: do individuals rely on information about the past behaviour of others (public information)? [5] Cross-generational reciprocity does not require such information, whereas image scoring does. An asterisk (*) indicates parameter combinations for mechanisms of cooperation that have not yet been explored theoretically.

four key issues: the presence or absence of investment, return investment, direct or indirect interactions and positive or negative control mechanism. We suggest that these issues capture the key differences between some main concepts in the literature on the evolution of cooperation among non-relatives and explain how these concepts are linked. We then turned to three of the most popular hypotheses involving direct benefits in the cooperative breeding literature, namely ‘pay-to-stay’, ‘group augmentation’ and ‘social prestige’. Our analyses indicate that (a) these hypotheses can be categorised in the same way as more general mechanisms for the maintenance of cooperation, but that (b) each hypothesis may in fact subsume several distinct mechanisms. The first result appears to justify a closer integration of studies of cooperative breeding with analyses of the evolution of cooperation. Cooperative breeding provides an ideal context in which to study the partner control mechanisms that promote cooperative behaviour in animals. Hence, it is puzzling that the rich empirical evidence in this field has remained largely separated from cooperation theory (but see Brown, 1987; Clutton-Brock and Parker, 1995; Connor, 1995b; Clutton-Brock, 2002). Despite the many aspects of cooperative behaviour that are potentially involved in cooperative breeding, reviews of the evolution of cooperation tend to ignore cooperative breeding or explain it as a whole in terms of one particular mechanism, e.g. by-product mutualism (Sachs et al., 2004). We hope that this will change in the future. Our second result may alert empiricists to the fact that current theories of cooperative breeding are poorly defined. Each of the issues we have addressed must be carefully investigated to allow a thorough understanding of the game structure. In particular, group augmentation has to

be explored in much more detail if we are to understand fully the evolutionary stability of investments in the system under study. Other concepts proposed in the cooperative breeding literature may also be analysed in the same way in the future, including task sharing (Taborsky, 1994; Lacey and Sherman, 1997; Clutton-Brock et al., 2003; Arnold et al., 2005), redirected helping (Emlen, 1982; Dickinson and Hatchwell, 2004), strategic between group dispersal (Bergmüller et al., 2005a), load lightening (Crick, 1992; Heinsohn, 2004), kinship deceit (Connor and Curry, 1995), parental facilitation (of territorial inheritance) (Brown and Brown, 1984), skill acquisition (Brown, 1987; Komdeur, 1996) and between group competition (Brooke and Hartley, 1995; Cockburn, 1998).

5.1. How to study cooperative behaviour in cooperative breeders?

The historical separation between cooperation and cooperative breeding seems at least partly due to differences in methodology. Empirical studies on cooperative breeding focus on ecological parameters and final net outcomes but usually not on the exchange of cooperative behaviours. Measured parameters include habitat saturation, dispersal patterns, survival probabilities of breeders, helpers and offspring, reproductive success of breeders with and without helpers, and finally direct comparisons of the inclusive fitness of same aged individuals that either help or breed independently. This approach differs markedly from empirical studies in general cooperation research in which researchers focus on the maintenance of cooperative behaviour studying the behaviour of individuals in very specific situations. The responses of individuals to each others' behaviour are then used to deduce the strategies individuals are using. This step is important as selection does not act at the level of interactions, but at the level of individual strategies (Noë, 2006). With this approach, fitness is never measured directly. Instead, the long-term association is split into multiple exchanges. Using this approach in cooperative breeding, one would observe how a breeder responds each time a helper provides food to its offspring, and each time the helper swallows the food itself. An experimental approach would be to induce a change in frequency of the two behaviours and to observe the reaction of the breeder (Bergmüller and Taborsky, 2005) (or vice versa, to manipulate the behaviour of the breeder, and observe the helper's response). Clearly, the fitness payoff of each single helper decision is small for any of the players involved (helper, breeder, offspring). However, it is simple to construct a payoff matrix in which the value is positive (versus negative) for the helper if it swallows the food (versus delivers the food to the offspring) and positive (versus negative) for the breeder if the helper delivers the food (versus swallows the food). After a long series of interactions the sum of the payoffs should have a substantial impact on the fitness of the players. In this case, helpers (in particular unrelated helpers but possibly also related ones) may increase their fitness by not providing any food, forcing breeders to find ways to control helper behaviour to ensure a significant contribution. As a consequence, one would expect to observe behavioural strategies of breeders that serve to promote

help, either by responding favourably to a helper that feeds the chicks or by inflicting some cost on a helper that fails to deliver food.

5.2. New avenues for theoretical research

Our approach highlights the need for specific models of cooperative behaviours involved in cooperative breeding. During our analysis several mechanisms emerged that seem to occur in cooperative breeding systems but have not yet been explored theoretically: indirect pseudo-reciprocity, negative pseudo-reciprocity and indirect reciprocity without image scoring (across generations). Even more importantly, it will be a challenge for theoreticians to explore the conditions favouring alternative mechanisms. For example, under which conditions should we expect negative reciprocity (punishment) instead of negative pseudo-reciprocity (eviction)? In addition, there are a number of as yet unresolved issues that need to be addressed. Three key issues are N-player interactions, the influence of outside options and symmetric versus asymmetric strategy sets. We consider it crucial that empiricists collaborate with theoreticians on these issues to generate a firm theoretical basis that closely corresponds to the phenomena observable in nature.

5.3. N-player cooperation

Although models of cooperation often focus on interactions between two individuals, cooperation may involve more than two individuals, resulting in N-player games. Almost by definition, cooperative breeding involves multiple players contributing to raising offspring, territory defence or other tasks. The conceptual problem with N-player cooperation is that individuals typically invest into common goods (the offspring, a territory, protection) that are shared among all group members. Theory predicts that cooperation should break down under these circumstances, a phenomenon first described as the 'tragedy of the commons' (Hardin, 1968). This is because no individual should invest into a common good if others (i.e. free-riders) could profit from this investment without contributing themselves. Despite this theoretical prediction, we often observe individuals investing in common goods in nature, for instance in cooperative territory defence, cooperative hunting or cooperative breeding. Current solutions to the tragedy of the commons in common goods games include, for instance, reputation (Milinski et al., 2002), and population dynamics in structured populations (Killingback et al., 2006 and cited references).

In cooperative breeders, many phenomena are for simplicity often treated as interactions between two individuals. For example, helpers may mainly interact with the breeder of the same sex, with helper contributions depending on the outcome of these interactions. On the other hand, many situations clearly involve interactions between more than two individuals, although it might be often difficult to determine which individuals actually do interact at any given point of time. Some phenomena appear to involve investment in a common good, e.g. the offspring or a territory. For instance, in bell miners (*Manorina melanophrys*)

helpers regularly provision young of different breeding pairs and also exhibit extreme cooperative group-defence, sometimes almost totally excluding other avian species from the colony's territory (Clarke and Fitzgerald, 1994). Categorising aspects of cooperative breeding as 2-player or N-player interactions makes a crucial difference with regards to cooperation theory. Therefore, examples like this suggest that more research is needed to determine in which instances N-player models are appropriate.

5.4. *Outside options: biological market theory*

Including the option to choose between partners (one possible outside option) remains a key challenge for future models of cooperation and is important for our understanding of payoff structures in cooperatively breeding systems. Besides influencing whether an individual will cooperate or not, choice options may also explain how much an individual will invest. For example, Noë (1990) witnessed a period in which a male baboon was the only possible alliance partner for two other males in the group. During this time period, the 'veto-player' male reaped almost all the benefits from the successful coalitions he engaged in with his two partners. In the cleaning mutualism, there is evidence that a shift from no partner choice to partner choice yields a shift from punishment as a control mechanism to partner switching (Bshary and Grutter, 2002a; Bshary and Schaffer, 2002). According to our classification tree, partner switching is an example of negative pseudo-reciprocity: a lack of investment by the cleaner leads the client to self-servingly choose another cleaner (in expectation of a better service), while its current cleaner incurs a cost (loss of a client) as a by-product. Thus, partner choice may influence payoff distributions among partners and may be an important mechanism in preventing partners from reducing their investment. We did not include partner choice as one of the building blocks in our decision tree because it may act in combination with any other mechanism in which investments are involved.

In cooperative breeders partner choice may have important consequences, for instance when helpers have the option to strategically switch to another group (Noë et al., 1991). According to biological market theory (Noë and Hammerstein, 1995; Noë, 2001) this option allows helpers to trade their helping contributions for acceptance in a territory that offers better conditions, e.g. due to a shorter queue for the breeding position or a lower workload than in the current group (Bergmüller et al., 2005a). Likewise, when breeders are in need of helpers they should adjust the level of help they demand from their helpers in order to forestall their dispersal when favourable alternatives are available. Therefore, researchers need to ask how easily breeders could choose other helpers and how easily helpers could switch to other breeders. The options for both sides are likely to change between years, depending on the ratio of breeders and helpers. Also, a helper's option to breed independently should influence the net investment it makes (Bergmüller et al., 2005b). Reproductive skew theory addresses this last issue but often without using biological market terminology.

5.5. *Symmetric or asymmetric relationships and interactions*

Classic cooperation theories like the prisoner's dilemma are built on the assumption that both players have identical strategic options (to cooperate or to cheat) and hence have identical problems to solve, possess identical power or are in identical states. However, asymmetries in these aspects are likely to be the norm rather than the exception in nature, e.g. when dominance hierarchies are involved or individuals vary in their age, condition or prior experience. Asymmetries between partners with respect to power may create asymmetries in the option to use punishment against cheating. However, asymmetries have as yet not been fully addressed in cooperation theory. Cooperative breeding is obviously full of asymmetries, most evidently, breeders are generally dominant over helpers. This often involves asymmetries in the currencies exchanged, for instance helpers helping in exchange for tolerance by the breeders. Another key asymmetry concerns the strategic options of breeder and helper. For clarity, let us assume that a helper is unrelated to breeders and offspring. In the helper's ideal world, it could use the resources of the territory without providing any help. In other words, it would benefit from cheating. The breeder, however, lacks the option to cheat the helper in return. The breeder may use aggression to enforce investment by the helper, but only up to the point where a helper prefers to leave. The breeder may also be able to evict a helper from the territory. However, this is not cheating, as the breeder cannot remove the helper and receive additional help at the same time. Pay-to-stay and biological market models incorporate such asymmetries but otherwise such assumptions are still rare in cooperation theory (but see Johnstone and Bshary, 2002).

5.6. *Interactions of kin based and non-kin based cooperation*

Mechanisms that provide direct and indirect benefits to helpers or dominants are for simplicity often regarded in isolation. However, it is clear that both types of mechanisms may often interact or act in parallel (Lehmann and Keller, 2006). One way to disentangle these mechanisms is to investigate species in which related and unrelated helpers are present simultaneously and to analyse the amount of help provided by both types. While related helpers are already an indirect benefit to dominants by their mere existence, unrelated helpers may be expected to engage more extensively in helping to compensate for the possible costs they impose on the breeders. However, in pied kingfishers, for instance, unrelated secondary helpers help less than related primary helpers (Reyer, 1984). Several studies of cooperative birds and mammals have shown that helpers which are unrelated to the young they are raising invest equally as closely related helpers (Dunn et al., 1995; Magrath and Whittingham, 1997; Clutton-Brock et al., 2000).

One framework to treat interactions between direct and indirect benefits are reproductive skew models (Johnstone, 2000; Magrath et al., 2004). We propose future theoretical and empirical studies are needed to determine the relative importance of investments due to direct, indirect or combined returns.

5.7. Kinship, interdependence and the value of lasting associations

Kinship has been interpreted recently as a special case of interdependence (the fitness of one individual depends on the fitness of another), resulting in an interest or ‘stake’ of the altruist in the fitness of the beneficiary (Roberts, 2005). While inclusive fitness theory addresses interdependence solely with respect to genetic relatedness, it can also prevail in general if an altruist benefits as a secondary consequence of helping (i.e. due to a by-product). Therefore, altruistic behaviours can be favoured if their costs are outweighed by the altruist’s stake in the beneficiary. According to this view, an investment in a relative is a special case of pseudo-reciprocity, where the resulting by-product benefits are due to the genetic benefits accrued through the increased fitness of the recipient.

Interdependence between individuals should have general implications for the stability of cooperative behaviour. It may explain individual investments, even if they do not result in direct responses on investments (i.e. like in reciprocity). This is the case, for instance, when individuals live in the same groups and benefit from the mere presence of others (e.g. by predator dilution) or when social relationships have a value (Aureli, 1997), e.g. when individuals are interdependent due to familiarity (Bergmüller et al., 2005a) or social bonds (Brown, 1987). This should be relevant in group living animals like cooperative breeders, where investments may often be based on lasting relationships between individuals who are concerned with the costs and benefits of interactions on a much longer time scale than that of a single exchange (Packer and Pusey, 1997; van Schaik and Kappeler, 2006). Therefore, interdependencies between interaction partners such as social relationships have to be taken into account when using a game theoretical approach, as they may influence an individual’s investment and choice of behaviour in any given situation.

6. Conclusions

We have attempted to relate existing theories for the evolution of cooperation and concepts from the distinct field of cooperative breeding. We suggest that this integrative approach may be useful in creating a unified framework that allows us to analyse different forms of cooperation in a more consistent way. We emphasise that cooperative breeding offers an ideal context in which to test more general theories of cooperation, provided that it is studied at all the appropriate levels, i.e. also focusing on the responses of individuals to changes in the behaviour of others, and not simply on the net outcome of the interaction. Finally, we believe that our systematic approach highlights a number of issues (both theoretical and empirical) that remain to be tackled before a comprehensive understanding of cooperation, including cooperative breeding, can be achieved.

Acknowledgements

We would like to extend our thanks to all those who attended and contributed to the workshop of the 11th Congress of the

ISBE in Tours. Katharina Peer provided helpful comments on an earlier version of the manuscript. Our collaboration was supported by Behavioural Processes. R. Bergmüller was further supported by the Suisse National Science Foundation SNSF grant 3100A0-108019 to R. Bshary, and AFR by the Royal Society.

References

- Alexander, R.D., 1987. *The Biology of Moral Systems*. Aldine de Gruyter, New York.
- Arnold, K.E., Owens, I.P.F., Goldizen, A.W., 2005. Division of labour within cooperatively breeding groups. *Behaviour* 142, 1577–1590.
- Aureli, F., 1997. Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggressive Behav.* 23, 315–328.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Balshine-Earn, S., Neat, F., Reid, H., Taborsky, M., 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping in a cooperatively breeding fish. *Behav. Ecol.* 9, 432–438.
- Bergmüller, R., Heg, D., Peer, K., Taborsky, M., 2005a. Extended safe havens and between group dispersal of helpers in a cooperatively breeding cichlid. *Behaviour* 142, 1643–1667.
- Bergmüller, R., Heg, D., Taborsky, M., 2005b. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proc. R. Soc. Lond. B* 272, 325–331.
- Bergmüller, R., Taborsky, M., 2005. Experimental manipulation of helping in a cooperative breeder: helpers ‘pay-to-stay’ by pre-emptive appeasement. *Anim. Behav.* 69, 19–28.
- Bergstrom, C.T., Bronstein, J.L., Bshary, R., Connor, R.C., Daly, M., Frank, S.A., Gintis, H., Keller, L., Leimar, O., Noë, R., Queller, D.C., 2003. Group report: interspecific mutualism—puzzles and predictions. *Genet. Cultur. Evol. Coop.*, 241–256.
- Brockmann, H.J., 1997. Cooperative breeding in wasps and vertebrates: the role of ecological constraints. In: Choe, J.C., Crespi, B.J. (Eds.), *Social Behaviour in Insects and Arachnids*. Cambridge, pp. 347–371.
- Bronstein, J.L., 2001. The exploitation of mutualisms. *Ecol. Lett.* 4, 277–287.
- Brooke, M.D., Hartley, I.R., 1995. Nesting Henderson reed-warblers (*Acrocephalus vaughani taiti*) studied by DNA fingerprinting: unrelated coalitions in a stable habitat? *Auk* 112, 77–86.
- Brown, J.L., 1983. Cooperation: a biologist’s dilemma. In: Rosenblatt, J.S. (Ed.), *Advances in the Study of Behavior*. Academic Press, New York, pp. 1–37.
- Brown, J.L., 1987. *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton, New Jersey.
- Brown, J.L., Brown, E.R., 1984. Parental facilitation—parent-offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.* 14, 203–209.
- Bshary, R., Bronstein, J.L., 2004. Game structures in mutualistic interactions: what can the evidence tell us about the kind of models we need? *Adv. Study Behav.* 34, 59–101.
- Bshary, R., Grutter, A.S., 2002a. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* 63, 547–555.
- Bshary, R., Grutter, A.S., 2002b. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. *Ecol. Lett.* 5, 130–136.
- Bshary, R., Grutter, A.S., 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biol. Lett.* 1, 396–399.
- Bshary, R., Noë, R., 2003. Biological markets—the ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In: Hammerstein, P. (Ed.), *Genetic and Cultural Evolution of Cooperation*. MIT Press, Cambridge, London, pp. 167–184.
- Bshary, R., Schäffer, D., 2002. Choosy reef fish select cleaner fish that provide high-quality service. *Anim. Behav.* 63, 557–564.
- Bull, J.J., Rice, W.R., 1991. Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* 149, 63–74.
- Cahan, S.H., Blumstein, D.T., Sundstrom, L., Liebig, J., Griffin, A., 2002. Social trajectories and the evolution of social behavior. *Oikos* 96, 206–216.

- Cant, M.A., Johnstone, R.A., 2006. Self-serving punishment and the evolution of cooperation. *J. Evol. Biol.* 19, 1383–1385.
- Carlisle, T.R., Zahavi, A., 1986. Helping at the Nest, Allofeeding and Social-Status in Immature Arabian Babblers. *Behav. Ecol. Sociobiol.* 18, 339–351.
- Clarke, M.F., Fitzgerald, G.F., 1994. Spatial-organization of the cooperatively breeding Bell Miner *Manorina-Melanophrys*. *Emu* 94, 96–105.
- Clutton-Brock, T., 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296, 69–72.
- Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Sharpe, L., Kansky, R., Manser, M.B., McIlrath, G.M., 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proc. R. Soc. Lond. B* 267, 301–305.
- Clutton-Brock, T.H., Parker, G.A., 1995. Punishment in animal societies. *Nature* 373, 209–216.
- Clutton-Brock, T.H., Russell, A.F., Sharpe, L.L., 2003. Meerkat helpers do not specialize in particular activities. *Anim. Behav.* 66, 531–540.
- Cockburn, A., 1998. Evolution of helping behaviour in cooperatively breeding birds. *Ann. Rev. Ecol. Syst.* 29, 141–177.
- Connor, R.C., 1995a. Altruism among non-relatives—alternatives to the prisoners-dilemma. *Trends Ecol. Evol.* 10, 84–86.
- Connor, R.C., 1995b. The Benefits of Mutualism—a conceptual-framework. *Biol. Rev. Cambridge Philos. Soc.* 70, 427–457.
- Connor, R.C., Curry, R.L., 1995. Helping non-relatives—a role for deceit. *Anim. Behav.* 49, 389–393.
- Crick, H.Q.P., 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis* 134, 56–61.
- Darwin, C., 1859. *On the origin of species by means of natural selection*. London.
- Dickinson, J.L., Hatchwell, B.J., 2004. Fitness consequences of helping. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Dugatkin, L.A., 1997. *Cooperation Among Animals. An Evolutionary Perspective*. Oxford University Press, Oxford.
- Dunn, P.O., Cockburn, A., Mulder, R.A., 1995. Fairy-Wren helpers often care for young to which they are unrelated. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 259, 339–343.
- Emlen, S.T., 1982. The evolution of helping. I. An ecological constraints model. *Am. Nat.* 119, 29–39.
- Emlen, S.T., 1995. An evolutionary theory of the family. *Proc. Natl. Acad. Sci.* 8092–8099.
- Emlen, S.T., 1997. Predicting family dynamics in social vertebrates. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology. An Evolutionary Approach*. Blackwell Science, Oxford, pp. 228–253.
- Emlen, S.T., Wrege, P.H., 1988. The role of kinship in helping decisions among white-fronted bee-eaters. *Behav. Ecol. Sociobiol.* 23, 305–315.
- Fisher, R.A., 1930. *The Genetical Theory of Natural Selection*. Dover, New York.
- Foster, K.R., Wenseleers, T., Ratnieks, F.L.W., 2006. Kin selection is the key to altruism. *Trends Ecol. Evol.* 21, 57–60.
- Gaston, A.J., 1978. The evolution of group territorial behavior and cooperative breeding. *Am. Nat.* 112, 1091–1100.
- Hamilton, W.D., 1963. The evolution of altruistic behaviour. *Am. Nat.* 97, 354–356.
- Hamilton, W.D., 1964. The genetical evolution of social behaviour I u. II. *J. Theor. Biol.* 7, 1–52.
- Hammerstein, P., 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: Hammerstein, P. (Ed.), *Genetic and Cultural Evolution of Cooperation*. MIT Press, Cambridge, London, pp. 83–93.
- Hardin, G., 1968. Tragedy of the commons. *Science* 162, 1243–1248.
- Hart, B.L., Hart, L.A., Mooring, M.S., Olubayo, R., 1992. Biological basis of grooming behavior in antelope—the body-size, vigilance and habitat principles. *Anim. Behav.* 44, 615–631.
- Hatchwell, B.J., Komdeur, J., 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* 59, 1079–1086.
- Heg, D., Bachar, Z., Brouwer, L., Taborsky, M., 2004. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 271, 2367–2374.
- Heg, D., Brouwer, L., Bachar, Z., Taborsky, M., 2005. Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour* 142, 1615–1641.
- Heinsohn, R., 2004. Parental care, load-lightening, and costs. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Heinsohn, R., Legge, S., 1999. The costs of helping. *Trends Ecol. Evol.* 14, 53–57.
- Johnstone, R.A., 2000. Models of reproductive skew: a review and synthesis. *Ethology* 106, 5–26.
- Johnstone, R.A., Bshary, R., 2002. From parasitism to mutualism: partner control in asymmetric interactions. *Ecol. Lett.* 5, 634–639.
- Johnstone, R.A., Bshary, R., 2004. Evolution of spite through indirect reciprocity. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 271, 1917–1922.
- Killingback, T., Bieri, J., Flatt, T., 2006. Evolution in group-structured populations can resolve the tragedy of the commons. *Proc. R. Soc. B-Biol. Sci.* 273, 1477–1481.
- Kokko, H., Johnstone, R.A., Clutton-Brock, T.H., 2001. The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* 268, 187–196.
- Kokko, H., Johnstone, R.A., Wright, J., 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behav. Ecol.* 13, 291–300.
- Komdeur, J., 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* 7, 326–333.
- Komdeur, J., 2006. Variation in individual investment strategies among social animals. *Ethology* 112, 729–747.
- Lacey, E.A., Sherman, P.W., 1997. Cooperative breeding in naked mole-rats: implications for vertebrate and invertebrate sociality. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 267–301.
- Lamprecht, J., 1978. The relationship between food competition and foraging group size in some larger carnivores. A hypothesis. *Zeitschrift Für Tierpsychologie* 46, 337–343.
- Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism—a general framework and a classification of models. *J. Evolut. Biol.* 19, 1365–1376.
- Leimar, O., Connor, R.C., 2003. By-product benefits, reciprocity, and pseudoreciprocity in mutualism. *Genet. Cultur. Evolut. Coop.*, 203–222.
- Ligon, J.D., Ligon, S.H., 1978. Communal breeding in Green Woodhoopoes as a case for reciprocity. *Nature* 276, 496–498.
- Lotem, A., Fishman, M.A., Stone, L., 2003. From reciprocity to unconditional altruism through signalling benefits. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 270, 199–205.
- Magrath, R.D., Johnstone, R.A., Heinsohn, R., 2004. Reproductive skew. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Magrath, R.D., Whittingham, L.A., 1997. Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behav. Ecol. Sociobiol.* 41, 185–192.
- Milinski, M., Semmann, D., Krambeck, H.J., 2002. Reputation helps solve the 'tragedy of the commons'. *Nature* 415, 424–426.
- Mueller, U.G., Rehner, S.A., Schultz, T.R., 1998. The evolution of agriculture in ants. *Science* 281, 2034–2038.
- Mulder, R.A., Langmore, N.E., 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* 45, 830–833.
- Noë, R., 1990. A Veto game played by baboons: a challenge to the use of the Prisoner's dilemma as a paradigm for reciprocity and cooperation. *Anim. Behav.* 39, 78–90.
- Noë, R., 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. In: Noë, R., van Hooff, J.A.R.A.M., Hammerstein, P. (Eds.), *Economics in Nature*. Cambridge University Press, Cambridge, pp. 93–118.
- Noë, R., 2006. Cooperation experiments: coordination through communication versus acting apart together. *Anim. Behav.* 71, 1–18.
- Noë, R., Hammerstein, P., 1995. Biological markets. *Trends Ecol. Evolut.* 10, 336–339.

- Noë, R., van Schaik, C.P., van Hooff, J.A.R.A.M., 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology* 87, 97–118.
- Nowak, M.A., Sigmund, K., 1998. Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577.
- Packer, C., Pusey, A.E., 1997. Divided we fall: cooperation among lions. *Sci. Am.* 276, 52–59.
- Pellmyr, O., Huth, C.J., 1994. Evolutionary stability of mutualism between *Yuccas* and *Yucca* Moths. *Nature* 372, 257–260.
- Reeve, H.K., 1992. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* 358, 147–149.
- Reyer, H.U., 1984. Investment and relatedness—a cost–benefit-analysis of breeding and helping in the Pied Kingfisher (*Ceryle-Rudis*). *Anim. Behav.* 32, 1163–1178.
- Ridley, J., Sutherland, W.J., 2002. Kin competition within groups: the offspring depreciation hypothesis. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 269, 2559–2564.
- Roberts, G., 1998. Competitive altruism: from reciprocity to the handicap principle. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 265, 427–431.
- Roberts, G., 2005. Cooperation through interdependence. *Anim. Behav.* 70, 901–908.
- Russell, A.F., 2004. Mammals: comparisons and contrasts. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Russell, A.F., Hatchwell, B.J., 2001. Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 268, 2169–2174.
- Sachs, J.L., Mueller, U.G., Wilcox, T.P., Bull, J.J., 2004. The evolution of cooperation. *Q. Rev. Biol.* 79, 135–160.
- Sherman, P.W., Lacey, E.A., Reeve, H.K., Keller, L., 1995. The Eusociality Continuum. *Behav. Ecol.* 6, 102–108.
- Stiver, K.A., Dierkes, P., Taborsky, M., Gibbs, H.L., Balshine, S., 2005. Relatedness and helping in fish: examining the theoretical predictions. *Proc. R. Soc. B-Biol. Sci.* 272, 1593–1599.
- Taborsky, M., 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Adv. Study Behav.* 23, 1–100.
- Trivers, R.L., 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46 (4), 35–57.
- van Schaik, C.P., Kappeler, P.M., 2006. Cooperation in primates and humans: closing the gap. In: Kappeler, P.M., van Schaik, C.P. (Eds.), *Cooperation in Primates and Humans*. Springer-Verlag, Heidelberg.
- Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. *Nature* 288, 850–852.
- West, S.A., Kiers, E.T., Simms, E.L., Denison, R.F., 2002a. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 269, 685–694.
- West, S.A., Pen, I., Griffin, A.S., 2002b. Cooperation and competition between relatives. *Science* 296, 72–75.
- West-Eberhard, M.J., 1975. The evolution of social behaviour by kin selection. *Q. Rev. Biol.* 50, 1–33.
- Wiley, R.H., Rabenold, K.N., 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* 38, 609–621.
- Wilson, E.O., 2005. Kin selection as the key to altruism: its rise and fall. *Soc. Res.* 72, 159–166.
- Wilson, E.O., Hölldobler, B., 2005. Eusociality: origin and consequences. *Proc. Natl. Acad. Sci. U.S.A.* 102, 13367–13371.
- Woolfenden, G.E., 1975. Florida scrub jay helpers at the nest. *Auk* 92, 1–15.
- Zahavi, A., 1995. Altruism as a handicap—the limitations of kin selection and reciprocity. *J. Avian Biol.* 26, 1–3.