

On the further integration of cooperative breeding and cooperation theory

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Abstract

We present a synopsis about the commentaries to the target article “Integrating cooperative breeding into theoretical concepts of cooperation”, in which we attempted to integrate general mechanisms to explain cooperative behaviour among unrelated individuals with classic concepts to explain helping behaviour in cooperative breeders that do not invoke kin-based benefits. Here we (1) summarize the positions of the commentators concerning the main issues we raised in the target article and discuss important criticisms and extensions. (2) We relate our target article to some recent reviews on the evolution of cooperation and, (3) clarify how we use terminology with regard to cooperation and cooperative behaviour. (4) We discuss several aspects that were raised with respect to cooperative interactions including by-product mutualism, generalised reciprocity and multi-level selection and, (5) examine the alternatives to our classification scheme as proposed by some commentaries. (6) Finally, we highlight several aspects that might hinder the application of game theoretical mechanisms of cooperation in cooperatively breeding systems. Although there is broad agreement that cooperative breeding theory should be integrated within the more general concepts of cooperation, there is some debate about how this may be achieved. We conclude that the contributions in this special issue provide a fruitful first step and ample suggestions for future directions with regard to a more unified framework of cooperation in cooperative breeders.

Keywords: Cooperative breeding; Cooperation theory; Pseudo-reciprocity; Reciprocity; Multi-level selection; By-product mutualism

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1. Introduction

The main aim of our target paper (Bergmüller et al., 2007) was to integrate some ‘classic concepts’ to explain cooperative behaviour between unrelated individuals in the field of cooperative breeding into ‘general’ cooperation theory. To identify the single components involved in cooperative interactions we argued that it is helpful to distinguish between interactions that involve: (1) no investment versus investment; (2) by-product benefits versus costly responses; (3) direct versus indirect responses and (4) positive versus negative control mechanisms. We found that (a) the concepts for direct benefits of cooperation in the field of cooperative breeding can be translated into mechanisms in cooperation theory; (b) some concepts in the field of cooperative breeding (pay-to-stay, group augmentation and prestige) are imprecise as they incorporate multiple mechanisms; and (c) some potentially important mechanisms in cooperation theory (e.g. negative pseudo-reciprocity (but see Hamilton (2007)), indirect pseudo-reciprocity and cross generational ‘reciprocity’) remain to be addressed theoretically. Finally, we argued that for a closer integration of both fields we need to pay more attention to the following future issues: (a) N-player interactions; (b) asymmetries between the players; (c) outside options/biological markets; (d) interactions of kin-based versus non-kin-based mechanisms of cooperation; and (e) interdependence between individuals.

We were encouraged by the responses; all commenters agreed that it is important to attempt to integrate the concepts used to explain helping in cooperative breeding within general cooperation theory. However, as one would expect, there is some debate about how this can be achieved. Some of the first authors for comments are also, or primarily, interested in cooperation theory (Connor, 2007; Hamilton, 2007; Kokko, 2007; Noë, 2007; Roberts and Sherratt, 2007; Sachs and Rubenstein, 2007; Skubic, 2007), but most commentaries were provided by empiricists in the field of cooperation, most of them working on cooperatively breeding species. These authors covered much of the broad spectrum of cooperatively breeding animal taxa ranging from social insects (Field and Cant, 2007; Korb and Heinze, 2007), fishes (Buston and Balshine, 2007; Hamilton, 2007; Skubic, 2007; Taborsky, 2007), birds (Berg and Williams, 2007; Cockburn, 2007; Covas et al., 2007; Doerr et al., 2007; Ekman, 2007; Hatchwell, 2007; Komdeur, 2007; Wright, 2007) to mammals (Connor, 2007; Gilchrist, 2007) including primates (Noë, 2007; Snowdon and Cronin, 2007) and humans (Kramer, 2007). We hope this joint effort will also contribute to close the prevailing gap between research on invertebrate and vertebrate cooperative breeding and foster communication between the fields.

Unsurprisingly, the commentators raised several issues we did not address in our target article. It is clearly beyond the

scope of our reply to address all the issues that were raised in the 22 commentaries. Instead, we ask the reader to read the commentaries her-/himself for some aspects that are missing in this synopsis. In order to give the reader some orientation about where to find which additions/criticisms, we sent out a questionnaire to the authors of commentaries, asking them (a) to explicitly state on which major points they agreed or disagreed with regards to our article and (b) to summarise the main message of the commentary in one sentence. Most authors replied. In Section 2 we provide the results of the questionnaire and address these results and other issues raised by the commentators that we consider particularly important or interesting. In Section 3 we position our target article relative to some recent reviews on cooperation. In Section 4, we re-address the issue of terminology. In Section 5 we attempt to clarify our position with regards to some basic disagreements on the various cooperation concepts of cooperation/cooperative breeding, and in Section 6 we discuss the proposed alternative classification concepts provided by the commenters. Finally, in Section 7 we discuss some factors that may hinder the application of game theory to cooperation in cooperatively breeding systems.

2. Summary of responses

As a response to our questionnaire, 20 out of the 22 authors (or groups of authors) returned the questionnaire. In general, the rate of agreement with regards to our main points was high (around 81%). However, a few points remained disputed (Table 1).

Our claim that it should be possible to describe the concepts that are used in cooperative breeding literature to explain helping in terms of ‘general’ cooperation language was the only subject of obvious disagreement with regards to our main points. We suspect, there are two main reasons for this: (1) a number of authors objected to our focus on mechanism of cooperation maintained by direct fitness benefits (hence our exclusion of kin based cooperation) with regards to the important mechanisms of cooperation (Korb and Heinze, 2007; Taborsky, 2007) and (2) the main mechanisms of cooperation appear too simplistic to describe complex patterns of cooperation as can be found in many cooperative breeders (see for instance the problem of N-player interactions, Cockburn, 2007). We will discuss these issues below. A third possible reason for why some authors disagreed with this point was perhaps the formulation “concepts can be ‘reduced’ to mechanisms of cooperation”. While we meant to ask whether the commenters agreed that the concepts in cooperative breeding can be ‘translated’ or ‘described’ in terms of general cooperation language, some authors might have understood a different meaning of the phrase. We have summarized the main message of the articles by the commentators in Table 2.

Naturally, the authors of the commentaries tended to focus on specific issues of our initial article or on how our article

Table 1
Short summary of the main points developed in each commentary

	I agree	Not sure	I disagree	No answer	%I agree
Main issues of the review					
Integration of cooperative breeding (CB) and 'general' cooperation are important	20	0	0	0	100
Concepts in the field of CB can be reduced to mechanisms of cooperation	8	2	10	0	40
Concepts in the field of CB are ill-defined, some incorporate multiple mechanisms	16	3	0	1	80
Some potentially important mechanisms have yet to be addresses theoretically	16	3	1	0	80
Average agreement					75
The following key distinctions are helpful to investigate cooperation in cooperatively breeding systems					
No investment vs. investment	16	2	2	0	80
By-product vs. costly response	16	2	2	0	80
Direct vs. indirect response	14	5	1	0	70
Positive vs. negative control mechanism	16	2	2	0	80
Average agreement					77.5
Some important future issues are					
N-player cooperation	15	5	0	0	75
Asymmetries	17	3	0	0	85
Outside options/biological markets	18	2	0	0	90
Interactions of kin-based vs. non-kin-based mechanisms of cooperation	19	1	0	0	95
Interdependence/long lasting relationships	19	1	0	0	95
Average agreement					88
Overall agreement					81

Table 2
The table summarizes the responses of 20 commentators to our questionnaire

Berg and Williams	We are constrained by our ability to collect the kind and quality of field data that would be necessary for effective integration of cooperation and cooperative breeding theory.
Buston and Balshine	The evolution of cooperative behavior can be understood by comparing payoffs of cooperative and alternative actions, accrued directly and indirectly, in present and future.
Cockburn	Because help inevitably involves interactions with two players (same sex and opposite sex dominant) it is impossible to portray the fitness outcomes as a dyadic interaction
Connor*	Invested, extracted and byproduct benefits: a modified scheme for the evolution of cooperation.
Covas, McGregor and Doutrelant	Communication network framework might help understanding cooperation in cooperatively breeding systems.
Doerr, Doerr and Safran	Cooperative breeding is more than just helping—delayed dispersal should also be integrated into broader theoretical work on social group formation.
Ekman	The four questions do not include the environment or design, but focus on fitness as an outcome of individual interactions.
Field and Cant	In primitively eusocial wasps, cooperation may have a limited role in explaining patterns of helping, but reciprocity is generally not involved.
Gilchrist	Communal breeding species with low reproductive skew need to be considered; defining and identifying the recipient of help is crucial to determining the game-theory pathway.
Hamilton	This is a helpful scheme for organising and clarifying theories CB, but CB societies involve complexities that are often not considered in more general theories of cooperation.
Hatchwell	The framework will help to clarify hypotheses for the evolution of cooperative breeding among unrelated individuals and identify avenues for future theoretical research.
Kokko*	Cooperative behaviour and cooperative breeding: what constitutes an explanation?
Komdeur*	Constraints on evolutionary shifts in cooperative breeding
Korb and Heinze	Dissecting without taking fitness into account might remain descriptive and limited to proximate aspects.
Kramer	The framework proposed by the authors is valuable in helping to resolve the theoretic challenges of situating humans, who routinely rely on the nonmaternal help to raise offspring, in the framework of cooperative breeding.
Noë	Partner choice should play a more central role. Choice by breeders is virtually guaranteed if there are several potential helpers.
Roberts and Sherratt*	Cooperative reading: some suggestions for integration of the cooperation literature.
Sachs and Rubenstein	Helping behavior can evolve when there is kin structure, automatic benefits (byproducts), or reciprocation. Choice systems are critical mechanisms to limiting cheating.
Skubic	Understanding cooperative behaviour and building a cooperation theory of cooperative breeding requires inclusion of system dynamics and feedbacks.
Snowdon and Cronin	Cooperative behavior is linked with cooperative breeding and rewards to alloparents are much more important than punishments.
Taborsky	I criticize the neglect of important concepts (RS theory, generalized reciprocity) and propose a framework to explain non-kin cooperation by (1) reciprocity, (2) social prestige and (3) coercion.
Wright	The complexity of the scheme illustrates the current confusion within cooperative breeding, and omits important issues concerning social prestige and group augmentation.

We calculated the level of agreement as the proportion of 'I agree' responses out of 20.

*Denotes the title of the contribution of those authors who did not provide a summary of their commentary.

could be relevant to their particular field. For clarity, we had focussed on some mechanism to explain cooperative behaviour in cooperative breeding (group augmentation, pay-to-stay and social prestige) knowing that there are many other concepts to explain helping behaviour. Some authors (Field and Cant, 2007; Gilchrist, 2007; Hamilton, 2007; Taborsky, 2007) wondered how reproductive skew theory relates to our framework. Reproductive skew models integrate ecological, genetic and social factors in a single explanatory framework to explain the degree of partitioning reproduction among helpers and breeders (Emlen, 1997). Partitioning of reproduction may either be cooperatively involving a positive control mechanism (i.e. in complete control models of RS, also called concession, incentives or optimal skew models of RS), or it may be enforced, i.e. involving a negative control mechanism (restraint models of RS), or it may not be cooperative but a result of competition between helpers and breeders (tug of war models) (Johnstone, 2000; Magrath et al., 2004). Restraint models of reproductive skew show obvious parallels to pay-to-stay based explanations for helping (Kokko et al., 2002; Bergmüller and Taborsky, 2005; Hamilton and Taborsky, 2005b).

Snowdon and Cronin (2007) and Sachs and Rubenstein (2007) highlight that ‘gain in experience’ may be an important factor promoting helping (Skutch, 1961; Brown, 1987; Komdeur, 1996). A conceptual problem with the ‘experience hypothesis’ is that it remains unclear why parents should risk the health/life of their offspring so that helpers may practice. We also wish to point out that conclusive evidence on experience gain can only be acquired by showing experimentally that engaging in helping promotes helping proficiency. Correlational evidence will always be confounded by differences in condition and quality. With respect to game theoretic concepts, experience gain qualifies as by-product mutualism: the helper gains the benefits (experience) directly through the act of helping, the benefits of this gain in experience do not depend on the actual survival and future behaviour of the offspring (as would be the case in pseudo-reciprocity). As yet, no study has used experiments to distinguish whether experience gain is a cause or a consequence of helping, or whether experience can be gained by simply delaying dispersal and watching successful breeders (Russell, 2004).

Noë (2007) emphasized the importance of partner choice for an understanding of interactions in cooperative breeders because the level of investments should be shaped by outside options when there is (a) more than one helper, (b) there is conflict between helpers and breeders and (c) when there is a power asymmetry between helpers and breeders (see also Noë et al., 2007). For instance, if there is a high supply in helpers and therefore great demand for access to a territory, market theory predicts that helpers should pay more to be allowed to remain in the territory because there are many other candidates queuing for the breeding position. Market conditions can thus lead to shifts in the payoff matrix. Skubic (2007) highlighted that helping and other behaviours are state dependent. Consequently, the ‘price’ a helper will pay for group membership at any given point of time depends on the helpers’ and breeders’ current state, but the value of help will also change dynamically over time. Partner choice

can also yield partner switching as the control mechanism that promotes cooperative behaviour (Bshary and Schaffer, 2002; Ferrière et al., 2002). Partner switching is equivalent to negative pseudo-reciprocity: in case of failure to invest the partner will selfishly end the interaction/relationship and start a new one with another individual.

Cockburn (2007) pointed out that cooperative breeders are often characterized by complex N-party interactions and illustrated this with Dunnocks and Superb fairy-wrens. He concludes “cooperative breeding is never a two-party game” and extends this critique to most of the currently available models of reproductive skew. We agree, but also highlight that recent studies have started to investigate the complexities arising when several players are involved, e.g. due to third party interactions. For instance, Hamilton and Heg (2007) show that, in addition to the interactions between male breeder and helpers, the behaviour of female breeders or more generally third parties can critically influence the outcome of the game (see also Hamilton, 2007). Therefore, we suggest the solution to treating N-party games is not to conclude that these interactions are too complex to be studied by a game theoretic approach. Instead, we need novel theoretical approaches to determine the effects of third party influences and N-player games.

3. Comparison of our target article to some recent reviews

Other conceptual papers on classifications and terminology of cooperation have recently been published (Lehmann and Keller, 2006; West et al., 2007) and Kokko (2007) suggests a meta-review on these and our target article would be helpful for an understanding of the differences between the approaches and the connections between them. While it is beyond the scope of this synopsis to provide such a review, we will briefly relate them to our target paper.

West et al. (2007) address the question of semantic confusion in the cooperation literature and Lehmann and Keller (2006) classify the existing models of cooperation within a general framework. Both demonstrate that with respect to evolutionary pathways, the situation is simple: the actor must gain fitness benefits either directly (“cooperation”) or indirectly (“altruism”) from investing, while the recipient always gains direct fitness benefits.

Similar to our approach, Lehmann and Keller (2006) distinguished between four different classes of models to explain cooperative behaviour, both with respect to cooperation, i.e. (a) “direct benefits” (no repeated interactions), (b) “reciprocation” (repeated interactions), as well as with respect to altruism, i.e. (c) kin selection and (d) green beard. We only dealt with the direct mechanisms of cooperation and in that respect their distinction is similar to ours: “direct benefits” is in our terms pseudo-reciprocity (including its variations) and “reciprocation” would in our terms refer to all interactions where the decision to invest depends on return investments (i.e. reciprocity and its variations).

With regards to direct benefits, West et al. (2007) distinguished between “non enforced” and “enforced”. What we

called by-product mutualism and positive pseudo-reciprocity (direct and indirect) would fall into their first class “non-enforced” while any form of reciprocity falls into the second class “enforced”. Therefore, overall, both Lehmann and Keller (2006) and West et al. (2007) are similar to our view in their discussion with regards to direct mechanisms to explain cooperative behaviour.

However, the goals of all three papers were different. While Lehmann and Keller (2006) and West et al. (2007) investigate evolutionary pathways to cooperation including direct and indirect routes to cooperation, we were analysing strategies or mechanisms that stabilize cooperative behaviours using a game theoretic approach, thereby specifically focussing on how an individual can increase its direct fitness in different types of interactions. In the literature there are three main answers to this question: (1) the behaviour is no investment because the benefit of the act is higher than its cost (i.e. it is self serving), irrespective of the recipient’s behaviour, i.e. by-product mutualism (West-Eberhard, 1975; Brown, 1983). (2) There is an investment into by-product benefits: the investment increases the by-product benefits the investor obtains due the self-serving behaviour (Cant and Johnstone, 2006) of the beneficiary, i.e. pseudo-reciprocity (Connor, 1986, 1995). (3) There is an investment that provides a benefit only if there is a return investment (by the recipient or by third parties), i.e. reciprocal strategies (Trivers, 1971; Alexander, 1987; Connor, 1995; Nowak and Sigmund, 1998). Evolutionary pathways and strategies/mechanisms promoting cooperative behaviour are complementary issues. Although each issue can be addressed separately, ultimately we have to understand both aspects.

4. Terminology

4.1. Classification scheme for concepts of cooperation, a clarification

The terminology in cooperation theory is currently confusing (Noë, 2006; West et al., 2007). It appears that some authors therefore assumed that one of our main goals was to remove semantic confusion. This is not the case; too many terms have been used in various ways by various researchers (see Noë, 2006). Therefore, we decided to explain each concept we used by its unique combination of a few key parameters. We believe that the advantage of our approach is that we can build up the compound mechanisms (the concepts of cooperation) from element components (the parameters or key questions) that are explicit in their terminology. Notwithstanding, independently of how one wants to name each parameter combination, our decision tree highlights the number of different concepts that may potentially apply to real life interactions and our tree provides clear definitions for our terminology. For example, the way we use the term ‘punishment’, it is defined as a control mechanism that promotes an investment by a player who thereby avoids the negative consequences of a direct costly response on the part of its partner. The cooperative act is therefore an investment in order to avoid punishment in direct negative reciprocity. This approach seemed to us just a necessary basis for

our main goal; to show that only a few parameters suffice to translate the concepts to describe helping behaviour in cooperative breeding in terms of ‘general’ cooperation terminology. As we pointed out in our target article, group augmentation, pay-to-stay and social prestige can easily be phrased according to our parameter combinations, often yielding equivalents to existing concepts of cooperation but sometimes also resulting in parameter combinations that have not yet been explored theoretically. Many authors commented on our terminology, claiming that there was a more ‘obvious’ or ‘natural’ alternative, although symptomatic of the problem, none suggested the same alternatives. It seems obvious that the only solution to avoid semantic confusion is to define how the terms are used (see also West et al., 2007).

4.2. It is important to distinguish ‘cooperation’ from ‘cooperative behaviour’

We chose to distinguish between cooperation, which we defined as an interaction that yields a fitness benefit to both parties, from a cooperative act, which we defined as a behaviour that benefits another. Several of the commenters (see also Lehmann and Keller, 2006; West et al., 2007) disliked this distinction, and suggested that it was “needlessly complicated” or “confusing”. We disagree. The distinction between the action of a single individual and the interaction between two individuals seems to us clear and inescapable. Certainly all of us will have had experience in investing in another individual in hope of a return on that investment which never materialised. In such situations we behaved cooperatively but the interaction was not cooperation. One can easily classify an action according to its fitness consequences for the actor and for the recipient – Taborsky (2007), for instance, describes an action as mutualistic if it has positive consequences for both, altruistic if it has positive consequences for the recipient but negative for the actor, parasitic if it has negative consequences for the recipient but positive for the actor, and spiteful if it has negative consequences for both. The fitness consequences of an interaction between two individuals, however, depend on the actions of both. Consequently, an interaction may yield positive fitness consequences for both players even if their individual actions do not. Suppose, for instance, that both individuals behave cooperatively, each conferring a benefit b on the other at a cost c to themselves. If $b > c$ then the result of the interaction is that each player obtains a net benefit $b - c > 0$, despite the personally costly nature of their actions. Similarly, suppose that both individuals behave in a self-serving manner, each obtaining a benefit b for themselves at cost c to the other. Again, if $b > c$ then the result of the interaction is that each obtains a net benefit; in this case, the cooperative outcome is the result of mutual exploitation rather than mutual cooperation. One may even imagine an interaction in which one individual acts in a mutualistic manner, while the other acts parasitically, yet the outcome is beneficial to both. Perhaps there is no need to coin a series of new terms to describe all the various possible combinations of actions and outcomes. But there is a need to distinguish clearly between the fitness consequences of a single individual’s behaviour, and the fitness

consequences of an interaction between two or more individuals. When some authors are concerned with the former and others with the latter, the result can only be confusion. Therefore, we wish to emphasize there is a critical distinction between using the two terms because whether one seeks to explain cooperative behaviour or cooperation are ultimately two different issues.

5. Specific aspects with regards to cooperative interactions

5.1. *By-product mutualism: cooperation due to collateral benefits*

West et al. (2007) propose that we should use the term cooperation only if the behaviour involved has been “selected for because of its beneficial effect on the recipient”, i.e. it is an investment. We agree on the most fundamental aspect: some behaviour resulting in cooperation should have been selected for. In agreement with West et al. (2007) we do not believe that “an elephant defecating [a self-serving act] and thereby benefiting dung beetles” qualifies as a by-product mutualism because none of the behaviours has been selected for. Similar to Clutton-Brock (2002), we suppose that in many instances of by-product mutualism it is self-serving coordination that has been under selection (note that coordination can be either self-serving or an investment). For instance, we find it hard to imagine that groupers evolved cooperative hunting with moray eels (a different species, hence kin benefits can be excluded) partly because morays benefit from it (Bshary and Grutter, 2006). Hence, in such a situation each individual clearly coordinates due to self-serving reasons, i.e. it is by-product mutualism. In our view “selected because of the benefits for the recipient” applies only to pseudo-reciprocity or reciprocity while the purely self-serving aspect is the key component of by-product mutualism.

In contrast to West et al. (2007), we do not believe that cooperation should be restricted to interactions involving investments as selection may also favour self-serving behaviours that result in cooperation due to ‘collateral benefits’ for others. For instance, a self-serving behaviour, such as ‘joining a group’ in order to obtain the benefits of safety in a group may, at the same time, yield by-product benefits for the other group members (i.e. selfish herd effects (Hamilton, 1971)). Many benefits of group living like selfish herd, dilution, and predator confusion are due to the by-product benefits individuals obtain by simply being together, while selection acts on the coordination of activities and space use. To conclude, we believe it is fundamental to acknowledge that by-product benefits of self-serving behaviours are evolutionary relevant and may result in benefits for all involved parties, i.e. cooperation.

5.2. *Negative pseudo-reciprocity: can it alone lead to a cooperative equilibrium?*

Hamilton (2007) argued that negative pseudo-reciprocity alone could never lead to a cooperative equilibrium, because

cooperation under the threat of eviction (or suppression) needs to involve both: negative pseudo-reciprocity (the sanction itself) and positive pseudo-reciprocity, in which cost reduction leads to selfish tolerance on the part of the partner. He argues that pseudo-reciprocity involves two steps: (1) investment in the sanction and then (2) a return investment in cost reduction. The only guaranteed return from sanctioning is the direct benefit of evicting or excluding the subordinate. Similarly, if the subordinate helps, there is a return to the subordinate in form of reduced threat of eviction. Hamilton concludes, if one reduces negative pseudo-reciprocity to only one step, that step is eviction, which is not in itself cooperative. We agree on this reasoning, but we also emphasized that ultimately, cooperative behaviour in negative pseudo-reciprocity can only be stabilized due to the threat of eviction, not by eviction itself (Bergmüller et al., 2007). Of course, this threat of eviction needs also to somehow come into being. As Hamilton (2007) points out, this may be a result of repeated suppression. But alternatives are possible too. For instance, an individual may have been ejected in another group and therefore knows about the cues that predict likely ejection. Alternatively, an individual might observe eviction of another individual and thereby learn about the consequences of not helping. Hence, although the act of terminating the interaction with one individual is not a cooperative act and does not result in cooperation, it can have the by-product effect of stabilizing cooperative behaviour in an audience. To conclude, we agree that negative pseudo-reciprocity alone does not lead to an interaction that can be called cooperation, but it is the threat of negative pseudo-reciprocity (or punishment), which can.

5.3. *Generalized reciprocity*

Generalized reciprocity results when B helps C because A helped B independently of the identity of individuals (Hamilton and Taborsky, 2005a; Pfeiffer et al., 2005; Rutte and Taborsky, 2007). There is evidence for generalized reciprocity in humans (Yamagishi and Cook, 1993) and rats (Rutte and Taborsky, 2007). It is related to kin selection because, ultimately, both rely on positive assortment of co-operators (Hamilton, 1975; Hamilton and Taborsky, 2005a; Lehmann and Keller, 2006). Both Skubic (2007) and Taborsky (2007) criticized our omission of generalized reciprocity, but unfortunately neither of both commenters discussed how generalized reciprocity could be acting in cooperative breeders. As interactions in cooperative breeders often take place between series of different individuals (i.e. helpers, breeders and offspring), generalized reciprocity could, most likely in addition to other mechanisms of cooperation, foster cooperation due to synergistic effects resulting from positive feedback. Also, it could be used as a flexible strategy enabling individuals to adjust to the current environmental conditions that result from the behaviour of the other individuals present, i.e. cooperate, when the environment is cooperative and, not cooperate, when the environment is non-cooperative. However, as yet the significance of generalized reciprocity in explaining cooperative behaviour in cooperatively breeding systems remains to be explored.

5.4. *Group augmentation: can it result from by-product mutualism?*

Several authors (Kokko, 2007; Roberts and Sherratt, 2007) criticized our proposal that ‘passive’ group augmentation could result from by-product mutualism. This is because group augmentation is a concept that intends to explain helping behaviour and therefore investments on the part of the helper. In ‘passive’ group augmentation (Kokko et al., 2001) a helper increases group size by helping to raise offspring in order to later obtain the (passive or by-product) benefits that result from living a larger group. The key question is whether the behaviour on the part of the helper is indeed an investment as the authors suggest, or a self-serving behaviour that produces the by-product effect of providing benefits to offspring. If one starts to define group augmentation as a concept to explain investments, we agree that the first interpretation must inevitably be the case. However, helping may not necessarily be an investment. Instead, it may also be a self-serving act, for instance in the context of territory defence. By defending the territory a helper will help augmenting the group because it profits directly, i.e. $b > c$, and the benefits conferred to the offspring are a by-product of self serving behaviour. This view is similar to ‘weak altruism’ were individuals provide group benefits due to self-serving reasons (on the population level) (West et al., 2007). As group augmentation is a common good problem, Wright (2007) argued it might require a multilevel selection explanation. Although this is an interesting possibility, ‘weak altruism’ can straightforwardly explain behaviours that confer group benefits as a result of individual selection promoting the behaviour due to the resulting direct benefits (see also Section 5.6).

5.5. *Prestige: the importance of signal reliability*

Wright (2007) emphasized it is crucial to acknowledge the signalling dimension with regards to prestige. The Handicap Principle, which has always been fundamental to social prestige theory (Zahavi, 1974, 1975, 1990; Wright, 1997, 1999), highlights that prestige can only be evolutionarily stable in cooperative breeding systems when there is signal reliability. According to the handicap principle, reliability can be achieved when the level of helping (a costly signal) reflects the condition dependent or genetic quality of the signaller. However, as Wright (2007) pointed out, the concept of prestige can become problematic to apply because signal reliability may become blurred in case additional factors critically influence the individual propensity to help. However, signal reliability may not necessarily be based on genetic quality. Client fish, for instance, base their decision about whether to interact with a particular cleaner on the service quality they observed in a previous interaction of the cleaner with another client (Bshary, 2002; Bshary and Grutter, 2006). Apparently, the current behaviour of the cleaner predicts to a certain extent how cooperative the following interaction will be, therefore eavesdropping on the interactions of others appears to contain reliable information for clients (Covas et al., 2007). Cleaners, in turn, can make use of an eavesdropping audience to signal their (short term) qual-

ity as cleaner (Bshary and Würth, 2001; Bshary, 2002; Bshary and D’Souza, 2004; Bshary and Grutter, 2006). Signal reliability is central for prestige based explanations of cooperative investment and it remains a challenging question to determine under which conditions signal reliability can evolve (see also Covas et al., 2007) so prestige can be an explanation of helping behaviour.

5.6. *Multilevel selection*

Group selection has been the focus of one of the largest controversies in evolutionary biology and the debate is still lively (Okasha, 2006). After Williams (1966) ended the era of ‘old group selection’, many scientists agreed that the appropriate level to study adaptation should be that of the individual. However, ‘individual’ is a somewhat arbitrary level of organisation and consequently researchers started to ask: why not the level of the gene, single cell or group of individuals? Much of the current debate on ‘modern group selection’ (also ‘trait group selection’ or ‘multilevel selection’) appears to linger upon the often vague definition of ‘individual selection’ (Okasha, 2006). Hence, a key question to ask is: what exactly is the individual level? Asking this question immediately forces one to focus on the level that should be exposed to the strongest effects of selection (although selection can simultaneously act on the other levels). Strong selection can act on groups of units when lower level units ‘sacrifice’ their individuality, or in other words, when there is strong interdependency between these units (Leigh, 1999), regardless of whether this interdependency is due to relatedness or other reasons (Roberts, 2005). For instance, genes are to a large extent interdependent within organisms, which means that the fitness of one gene depends on the fitness of other genes within the same individual. Similarly, the multilevel view has led to the sometimes fruitful concept of the ‘super organism’ in social insects, because individual colony members are strongly interdependent within the colony (Bourke and Franks, 1995; Korb and Heinze, 2004). Therefore, it seems important to ask how the concept of multilevel selection can be used to understand cooperative behaviour in other cooperative breeders (Kokko, 2007; Korb and Heinze, 2007; Hamilton, 2007; Wright, 2007).

With regards to multilevel selection as an explanation for the stability of cooperative behaviour, we recommend the papers by Lehmann and Keller (2006) and West et al. (2007). A basic conclusion of both papers is that the term ‘group selection’ can be confusing when it comes to evolutionary explanations of cooperation. Some reasons for the confusion are that researchers (1) tend to mix up ‘old’ and ‘new’ (multilevel) group selection, (2) avoid the use of ‘new group selection’ because they think it is unimportant (as they think is old group selection), (3) do not realize that kin selection theory and new group selection are just different ways to conceptualise the same issue: according to new group selection cooperation is favoured when increasing the genetic variance between groups compared to within groups, but this is precisely the same as increasing the kin selection coefficient of relatedness (Frank, 1995). (4) Because kin selection models appear often easier to apply (e.g. group selection tends to

hide the distinction between direct and indirect benefits), (5) it is sometimes argued that they are the ‘correct ones’ (see also West et al., 2007). However, in all cases where both methods have been used to study the same problem, the results obtained were equal (Frank, 1986; Bourke and Franks, 1995; Wenseleers et al., 2004; Gardner et al., 2007). Also, the multilevel approach provides the advantage that it allows to separate individual level and group level adaptations (Price, 1970; Hamilton, 1975; Foster, 2006). (6) Finally, a crucial source of confusion is that researchers often do not use Hamiltons’ original well defined terminology (see for details Okasha, 2006; West et al., 2007).

According to inclusive fitness theory, investments can be favoured due to direct (cooperative behaviour) or indirect (altruistic behaviour) fitness benefits due to shared genes (Hamilton, 1964). It is sometimes argued that altruistic behaviour can evolve without relatedness, but this results from using a ‘narrow’ definition of relatedness, i.e. due to recent common ancestry (e.g. Wilson and Hölldobler, 2005). However, when using the ‘broad’ definition (non zero relatedness between individuals) altruistic behaviour is by definition due to relatedness (Hamilton, 1964; Foster et al., 2006; West et al., 2007). West et al. (2007) illustrate in a very clear way how in ‘weak altruism’ (Wilson, 1980, 1990) an individual provides benefits to the group by incurring individual net costs on the group level, but at the same time acquiring direct net benefits on a population level. Therefore, when the conditions for ‘weak altruism’ are met (i.e. there is a sufficiently high synergistic effect of performing the act) group beneficial behaviour can result from direct benefits on the individual level. Although the behaviour appears altruistic at the group level, it is self-serving at the population level, and the benefits for other group members are a result of by-product mutualism (see also Lehmann and Keller, 2006). In contrast, any behaviour that on average reduces the (lifetime) direct fitness of the actor (i.e. it is altruistic) needs to increase the indirect fitness of the actor to be selected for (Lehmann and Keller, 2006).

Group selection theory is mathematically equivalent to inclusive fitness theory (Queller, 1992), i.e. both are combinations of kin selected and direct benefits. Therefore, kin selection theory and multi level selection are two compatible conceptualisations of the same issue, i.e. both concepts require a statistical tendency for the recipients of altruism to be altruists themselves (Hamilton, 1964, 1975). In physics, a pluralistic view of the nature of light has long been established: light can sometimes be best described as a particle but for other purposes the nature of light is best described as a wave (Penrose, 2005). Such thinking might also be helpful for evolutionary thinking: selection for altruistic and cooperative behaviour can sometimes best be conceptualised either with kin selection theory or with multilevel selection theory. Multilevel selection can be helpful to describe how selfish behaviours (i.e. self serving, but at a cost to others) of individual colony members in insect societies become suppressed, or in other words, cooperative behaviour is fostered (Reeve and Keller, 1997; Korb and Heinze, 2004). It will be a future challenge to determine how a multi level view can help to understand cooperative behaviour within cooperatively breeding vertebrates.

6. Alternative classifications schemes

Not surprisingly, many authors commented on our decision tree. Key critiques were that our tree is (a) too complex, (b) too abstract, and (c) misses important aspects. Alternative classifications were proposed by Buston and Balshine (2007), Connor (2007), Doerr et al. (2007), Noë (2007), Roberts and Sherratt (2007), Sachs and Rubenstein (2007), and Taborsky (2007). While each contributor felt that their classification is more ‘natural’, a comparison quickly reveals that what is natural remains a personal opinion as all proposals differ. We invite readers to compare for themselves and see what classifications they find useful. For our part, we do not believe that one can get away with a more simple classification than proposed in Bergmüller et al. (2007). The key distinctions – no investment versus investment, reciprocity versus pseudo-reciprocity, positive versus negative control mechanism, and direct versus indirect interactions – are all important in their own right, and all possible combinations have to be explored to place cooperative breeding firmly into cooperation theory. We also disagree with the critique that these concepts are too abstract or unnecessarily complex (Wright, 2007; Buston and Balshine, 2007). Concepts are supposed to be simplifications of the more complex real life, but simplifications that capture essential aspects of real life and theory driven research is the key strength in behavioural ecology.

Buston and Balshine (2007) propose the inclusion of indirect fitness benefits in our tree. However, our starting point was that many examples of cooperative breeding are not sufficiently explained with indirect fitness benefits and that our target paper addresses these cases. Following Hamilton (1964), direct and indirect fitness are additive. Therefore, an observed level of investment should have a direct and an indirect component as long as the interaction partners are related. We addressed this complication in the discussion but adding it to our tree does not help.

Sachs and Rubenstein (2007) doubt that the distinction between pseudo-reciprocity and by-product mutualism is an important one as in both cases, cheating is not a problem. While the latter statement is true, there is an important difference between the two concepts. In by-product mutualism individuals have gained at the end of the interaction (if what happens can be called an interaction). A player keeps this gain even if the partner drops dead the minute after. In positive pseudo-reciprocity, the observer has to look at the future behaviour of interactants to resolve the puzzle of investment, and temporal discounting (Stephens et al., 2002; Stevens and Hauser, 2004) may present a psychological barrier for this kind of cooperation in ‘more cognitive’ species. In negative pseudo-reciprocity, individuals cooperate to avoid negative consequences from self-serving behaviour of the partner, which is again very different from by-product mutualism.

Two alternative classifications were particularly interesting. First, Connor (2007), while agreeing with us on the four key parameters, proposed that the most important distinction is between positive and negative control mechanisms (extracted versus conferred benefits). We see advantages to his classification and to ours, and simply recommend the reader to compare

and to make up her/his own mind. Second, Roberts and Sherratt (2007) classified ‘direct versus indirect’ as the first key question to ask. They also use a different terminology: direct benefits are called ‘material benefits’, whereas indirect benefits are called ‘information’. Again, we see advantages and disadvantages with their classification compared to ours. The importance of information has also been emphasized by Wright (2007). However, information has to be transformed into material benefits at some point, otherwise the system would not work. In addition, contrary to the classification proposed by Roberts and Sherratt (2007), we feel that one should emphasize the differences between image scoring and prestige (competitive altruism) rather than highlighting the similarities. In competitive altruism, the observer uses the information to its own immediate benefit (it chooses a cooperative partner), whereas in image scoring, the observer uses the information to invest into its own image score by helping a cooperative individual. The latter is a form of reciprocity, the former a form of pseudo-reciprocity. Hence, agreeing with several commentaries that pointed out that pseudo-reciprocity is more stable than reciprocity, competitive altruism should be found much more often in nature than indirect reciprocity based on image scoring.

A special merit of the alternative scheme proposed by Roberts and Sherratt (2007) is that it includes N-player interactions. This was a major shortcoming of our tree, as most openly expressed by Cockburn (2007). We therefore appreciate very much their addition. While this makes the decision tree even more complicated, we insist that simple classifications (Buston and Balshine, 2007; Noë, 2007) or the restriction to an operational definition (Taborsky, 2007) fail to capture what we would like to know. The diversity of routes to cooperation cannot be simplified without losing key information on the systems; we can only try to link all routes in a global scheme that may explain the similarities and differences between them.

7. Aspects that may hinder the application of game theory

7.1. Consequences of inflexibility and constraints for cooperation

Several authors commented that individuals might be less flexible in their decision whether to cooperate or not than is assumed when taking a game theoretical perspective. For instance, (a) phylogenetic constraints might predispose individuals of a species to behave cooperatively or not (Kokko, 2007; Ekman, 2007). (b) The decision to help and to disperse may be closely linked, even if both decisions have different causes (Doerr et al., 2007; Ekman, 2007; Kokko, 2007; Noë, 2007). (c) Komdeur (2007) pointed out, that our assumption that individuals do have a capacity to flexibly react to the behaviours of other individuals might not always be fulfilled (see also Ekman, 2007). This is because individuals often consistently differ in their behavioural phenotype and that the way how they cope with environmental challenges often correlates across functionally independent contexts or situations. Such ‘behavioural syndromes’ or ‘animal personalities’ portray a limited flexibil-

ity in phenotypic behavioural adaptation that produces different types of individuals (Drent et al., 2003; Sih et al., 2004; Bell, 2007). Up to now, empirical research in cooperation and cooperative breeding has largely ignored the possibility of consistent inflexible types such as ‘cooperators’ and ‘defectors’ or different types of cooperators resulting in different behavioural roles in social groups (but see Arnold et al., 2005; Komdeur, 2006; Bergmüller and Taborsky, in review; Komdeur, 2007). Future research will need to take into account the consequences of such inflexibilities for a conclusive understanding of the question: why cooperate? This is because (a) the reasons for such individual inflexibilities are as yet largely unresolved and (b) their consequences of inflexibilities, such as ‘cryptic task sharing’ (Bergmüller and Taborsky, in review) due to different behavioural roles are only starting to become evident. To conclude, inflexibilities or constraints may crucially determine some of the variation in cooperative behaviour between individuals. Therefore, they must be taken into account when using game theory to study cooperative behaviour.

7.2. Who are the players?

Some commenters (Gilchrist, 2007; Field and Cant, 2007) correctly pointed out that the mechanism invoked to account for a cooperative behaviour relies upon knowing who the recipient of the act is. In two-player games recipients of interactions are obvious. However, as cooperative breeding by definition involves more than two players (minimum: one or two breeders, a helper and one offspring) (Berg and Williams, 2007; Cockburn, 2007; Gilchrist, 2007) the situation is more complicated and identifying the recipient of help can be problematic and depending on who is the recipient, the mechanism of cooperation can differ.

In practice, the true recipients of care can be difficult to identify. Suppose we have players B (the breeder), O (the offspring of the breeder), H (the helper) and O’ (the future offspring of H). Suppose also, that we are concerned with explaining the maintenance of a cooperative act in a species that benefits from living in large groups (i.e. individuals of the species benefit from augmenting group size). In such systems, the distribution of help is seldom ‘reciprocal’ in a narrow sense. Instead, help is often exchanged between series of different individuals (e.g. H helps O, therefore B tolerates H, etc.) even between generations. Also, the recipients of cooperative acts are not always obvious and commonly involve more than one individual. Below we illustrate these points in two examples.

- (1) Helper (H) could provide food directly to the breeder (B), allowing the B to increase the survival probability of offspring (O), which in turn increases the probability that O will provide food to H when H becomes a breeder at a later date. In this situation, we could conclude that the initial cooperative act (H feeds B) is maintained through indirect reciprocity (i.e. O feeds H because H fed B), but differs from ‘classic’ indirect reciprocity as image-scoring is not required to stabilize helping behaviour.
- (2) Alternatively, if helper (H) provides food directly to the offspring (O), and at some later point, the offspring (O) pro-

vides food to the offspring of the helper (O'), we might conclude that the initial cooperative act of H is maintained through generalized reciprocity (i.e. H helps O and as a consequence O helps O'). Again, this generalized reciprocity differs from 'classic' generalized reciprocity because it also involves kin selected benefits (i.e. H and O' are related) and because there is a large time delay between the cooperative acts of H and O. These two examples illustrate that in order to understand the mechanism through which the initial cooperative act is maintained, it is important to identify the receiver(s) of benefits.

Of course, as has been pointed out (Berg and Williams, 2007; Cockburn, 2007; Gilchrist, 2007), identifying whom the cooperative act is directed towards is problematic because a cooperative act may have (a) unobvious (for instance, resulting from by-products) or (b) multiple beneficiaries. The case of unobvious beneficiaries can be exemplified most simply by complete breeder load-lightening. For example, if H's investment towards O influences the behaviour of B such that B reduces its investment to O by the same amount as provided from H to O, the primary beneficiary of H's investment may be identified as actually being B not O. Whether we categorise the beneficiary in this case as O or B has a significant effect on the route through which the cooperative act by H is maintained. If we assume that the cooperative act is directed towards O, then H later benefits as a by-product of self-serving actions of a third party (i.e. the increased reproductive output of B), then the initial cooperative act can be explained through indirect pseudo-reciprocity. In other words, although H invests in O, it is B and not O that provides the benefit to H, by self-servingly producing more offspring. Interestingly, there is no information required for stable cooperation in this interaction. If, by contrast, we take the position that the cooperative act (although provided to the offspring) is actually directed towards the breeder (e.g. because providing food to the offspring is the most efficient way of helping the breeder), the third party is removed from the equation and hence the initial cooperative act is maintained through pseudo-reciprocity.

Finally, while in some species, complete load-lightening has been documented, it is more common for load-lightening to be incomplete (Hatchwell, 1999). In such situations, the provisioning of food from a helper to offspring has more than one beneficiary. In other words, if H provides O with food, both O and B benefit. Consequently, the initial cooperative act of H is maintained both through indirect and direct pseudo-reciprocity (see above). Such examples illustrate that the consequences of the cooperative behaviours need to be considered with regards to all potential beneficiaries in order to be able to classify the interaction to one or several concurrently acting mechanisms of cooperation.

8. Conclusions

There seems to be wide agreement that integrating the fields of cooperative breeding and 'general cooperation theory' is necessary. However, as demonstrated by the commentaries, there is

still a significant debate about how this could be achieved. We believe the contributions in this special issue provide a first step into a fruitful direction and opened up a field of potentially productive debate that will help to understand and integrate the underlying principles with regards to cooperation in cooperatively breeding systems.

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