

Commentary

Cooperation built the Tower of Babel

Michael Taborsky

Behavioural Ecology, University of Berne, Wohlenschtrasse 50a, CH-3032 Hinterkappelen, Switzerland

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According to the narrative in the genesis the Tower of Babel was built in a cooperative effort by a united humanity to reach the heavens. God, disapproving this intention confused the tongues of the builders and hindered further cooperation to complete their aim.

West et al. (2007) and Bergmüller et al. (2007) strived to confuse our tongues and turn “cooperation” into a faux-pas word. You certainly know the feeling when the pen in your hand is not moving as required because the word you intend to put down on paper is so nasty, scandalous or politically incorrect that you fear someone could suddenly peek over your shoulders and see the condemnable? The rather innocent and hitherto positively felt term “cooperation” is in danger to mutate to such a taboo. West et al. (2007) “prefer that a behaviour is only classed as cooperation if that behaviour is selected for because of its beneficial effect on the recipient.” Bergmüller et al. (2007) go further and propose that a distinction should be made between the words “cooperation”, which should in their view denote “an interaction between individuals that results in net benefits for all of the individuals involved” from “cooperative behaviour”, which they define “as an act performed by one individual that increases the fitness of another”, allowing to have either a direct positive or negative effect on the actor’s fitness. This means that “cooperative interaction” and “cooperative action” has no similar meaning any more—in the first case, fitness consequences need to be positive to both parties, while in the second case only one party needs to benefit while the other one can be subject to any fitness consequences, including none.

Now, when your 3-year-old daughter is helping you doing the dishes, this cannot be called cooperation any more. It cannot be called a “cooperative behaviour” or “help” either, because ultimately, her well-intended behaviour will probably not affect the recipient (and perhaps also the donor) in any positive way. Poor little thing, how can we call her behaviour then? Byproduct-pseudo-mutualism, or – more simply – spite?

Brethren hear my prayer: keep thy hands off terms used in everyday speech, or the consequence is unholy confusion. Alas, how often is this commonplace of scientific language needlessly neglected!

1. Intraspecific mutualism and parasitism

Let us call a spade a spade. In science we distinguish proximate and ultimate levels of analysis, and in our language there is descriptive and functional terms and for many matters we need both. What we are searching for here is an adequate functional term for the case that an individual spends effort to the benefit of itself and a conspecific. Snitching descriptive terms from everyday language is not a solution. However, adequate terms are readily available (Table 1). West et al. (2007) propose “mutual benefit” for this “behaviour”, which is close to what I would propose, but not absolutely right. A “benefit” is neither behaviour nor a collective term for a specific type of interaction. In my view the correct term is mutualism. This term is derived from latin “mutuus” for mutuality, i.e. two or more partners acting to their mutual benefit, and is in biology mainly used for interspecific relationships—but not only so (cf. West-Eberhard, 1975; Brown, 1983; Krebs and Davies, 1993; Clements and Stephens, 1995; Emlen, 1997; Clutton-Brock, 2002; Kalmbach et al., 2005; Ratnieks, 2006). I suggest to use the term mutualism for actions taken to benefit oneself and a partner (+/+), and to be clear about whether interspecific or intraspecific relationships are considered, one can add these adjectives accordingly. The corresponding term denoting interactions where the actor is exploiting its partner by a behaviour that benefits the former at the cost of the latter is parasitism (+/–). Also this term is most frequently used for interspecific relationships in biology, but not confined to them (e.g. Taborsky, 1997; Shine et al., 2003; Lopez-Vaamonde et al., 2004; Dietemann et al., 2006; Waldeck and Andersson, 2006). With the second line of this classification scheme, i.e. where the actor’s costs always outweigh its benefits derived directly from the act, there is less of a disagreement (but see West et al.,

E-mail address: michael.taborsky@esh.unibe.ch.

Table 1
Classification scheme with functional terms denoting social behaviours according to their fitness effects

Direct fitness effects of action	On recipient	
	Positive	Negative
<u>On actor</u>		
Positive	Mutualism (intraspecific or interspecific)	Parasitism (intraspecific or interspecific)
Negative	Altruism	Spite

2007 for discussion). These interactions are usually referred to as altruism (–/+) and spite (–/–), accordingly (see Table 1).

The term “by-product mutualism” has been used for situations “when individuals generate benefits to others as a by-product of performing a selfish act” (Bergmüller et al., 2007). Condition is, however, that this act does not involve “investment” (sensu Bergmüller et al., 2007), i.e. if two interacting partners coordinate their behaviour to some extent the term does not apply. Think of two lions or a pack of wolves running after their prey—they will always be influenced in their movement by the presence or behaviour of the other hunters, so there is no “by-product mutualism” involved. I regard this term useless for two reasons. First, it is not the “costs of investment” in coordination or other partner-directed behaviours that counts for the evolution of this form of mutualism, but the total direct cost of the act; the sum of direct costs of running behind an impala may be even smaller if a lion is joined by a conspecific despite some required coordinated movements than in single pursuit. Secondly, it will be hardly possible to measure “by-product mutualism” in any natural or semi-natural situation. There are more simple situations than cooperative hunting, but still, demonstrating that no change whatsoever is entailed in own (behavioural or other) costs by the presence or behaviour of a partner is extremely difficult to achieve.

The everyday word “cooperation” should remain at its established place—at the descriptive level. The simplest possible definition would be “acting together”, or “joint operation”. With more sophistication, Brosnan and de Waal (2002) termed cooperation “the voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have brought about individually”. Even though this definition inherently addresses fitness consequences (“benefits”), it does not confine the term to a specific direction of these consequences, hence it can be applied without (or before) knowing any fitness effects.

2. Beyond semantics

Bergmüller et al. (2007) propose also a lot of other terminology that might be worth discussing, but there are more interesting aspects on which to focus. The major aim of their paper is to draw attention to the fact that theory developed to explain cooperative behaviour and empirical studies of cooperatively breeding species run side by side, without taking notice of each other. They point out that a mutual approach has become urgent because

“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”. This is setting up an unfortunate – because needless – straw man. Despite the omnipresence of kin selection arguments to explain behaviour of cooperative breeders, individual or “direct” fitness benefits have been hypothesized for a long time to explain cooperation in advanced social systems, particularly in cooperative breeders (e.g. Gaston, 1978a,b; Ligon and Ligon, 1978, 1983; Rood, 1978, 1990; Woolfenden and Fitzpatrick, 1978; Reyer, 1980, 1984; Lawton and Guindon, 1981; Ligon, 1981; Rowley, 1981; Emlen, 1982; Taborsky, 1984, 1985; Brown, 1985, 1987, etc.). How recent is recent? Also, the “evidence for pay-to-stay ... [that] ... has recently begun to accumulate in a cooperatively breeding cichlid *Neolamprologus pulcher*” is in fact not really so recent (cf. Taborsky, 1984, 1985). The general point, however, is very worth to be made: surprisingly little communication seems to proceed between theoreticians modelling potential evolutionary mechanisms of cooperation and empiricists studying cooperation in highly social animals. The study of cooperation is indeed notorious in its deep divergence between theoretical concepts and equivalence in nature. While theoreticians indulge in the challenge of thinking about the unthinkable, empiricists usually lack the methodology to abstract general theoretical principles from the reality they observe and measure. A plea for both sides to cooperate is indeed more than obvious. And I think, the divergence extends far beyond terminology.

Surprisingly, though, Bergmüller et al. (2007) do not refer to reproductive skew theory, which is arguably the major theoretical concept developed to explain the evolution of cooperative breeding and eusociality (Vehrencamp, 1983; Reeve et al., 1998; Johnstone, 2000; Cant and English, 2006). Also, reproductive skew models allow to formulate precise predictions that can be tested by empirical studies (Reeve and Keller, 2001; Haydock and Koenig, 2002; Langer et al., 2004; Heg et al., 2006). One reason for this omission might be that skew theory largely confines its focus to the share of reproduction between group members. This does not suffice to explain sociality, and especially it does not help to understand the nature of cooperation involved in animal communities. Empiricists attempting to understand the nature of cooperation between wild animals focus on issues like the mechanisms underlying alliance formation and stability (e.g. Parsons et al., 2003; Lazaro-Perea et al., 2004; Silk et al., 2004; Connor et al., 2006), division of labour and behavioural specialization aiding cooperative coexistence (Clutton-Brock et al., 2004; Arnold et al., 2005; Nascimento et al., 2005; Komdeur, 2006; Sato and Saito, 2006), the importance of ecological and group characteristics for behavioural decisions in cooperative groups (e.g. Korb and Schmidinger, 2004; Bergmüller et al., 2005; Hamilton et al., 2005; Stiver et al., 2005; Kutsukake, 2006; Woxvold et al., 2006), reproductive roles (Dierkes et al., 1999; Awata et al., 2005; Gilchrist, 2006; Heg et al., 2006; Mori and Saito, 2006), the effects of cooperation (Hatchwell et al., 2004; Brouwer et al., 2005; Covas and du Plessis, 2005; Williams and Hale, 2006), mechanisms underlying group formation and structure (e.g. Tibbetts and Reeve, 2003; Heg et al., 2005; Sumana et

al., 2005; Stiver et al., 2006), and the nature of cooperative interactions between members of cooperative groups and alliances (e.g. Schino et al., 2003; Cronin et al., 2005; Kim et al., 2005; Kutsukake and Clutton-Brock, 2006). Reproductive skew theory addresses only a small fraction of these questions. Clearly, a different approach is needed.

3. Cooperation theory and the evolution of helpers at the nest

Bergmüller et al. (2007) propose to link the theory of cooperation with the studies of cooperative breeding. Much of this literature revolves around the tantalizing challenge to solve the iterated prisoner's dilemma game (Axelrod and Hamilton, 1981; Nowak and Sigmund, 1992; Killingback and Doebeli, 2002; Nowak et al., 2004). This literature has strongly influenced also the empirical research on cooperation. However, in this context behavioural strategies underlying cooperation have been frequently studied under very unnatural conditions, which may hamper interpreting the results (Clements and Stephens, 1995; Stevens and Stephens, 2004; Silk et al., 2005; Noe, 2006). There are notable exceptions, however, where models were generated to account for observed variation in behaviour among cooperative breeders or coalitions of unrelated conspecifics (e.g. Lucas et al., 1997; Cant and Field, 2001; Pandit and van Schaik, 2003; Skubic et al., 2004; Cant et al., 2006). Naturally, the general importance of such models is less clear than in fundamental models of evolutionary cooperation mechanisms. However, they dispose of the crucial advantage of reflecting a grain of reality, at least this is their aim. And they are experimentally testable under conditions that do not ask too much of the target animals (e.g. Cant and Field, 2005).

The hierarchical scheme proposed by Bergmüller et al. (2007) depends on the notion of “investment”. This is a critical factor, because it involves two elements: costs and intention; or the expenses entailed by an action, and its aim to benefit someone else. They define it as being a synonym for an “altruistic act” but add an essential component, the “expectation of a return”. I would propose to forbear from using the concept of investment in the classification scheme of cooperative relationships and rather stick to the conventional concept of “costs” and “benefits” to actors and recipients. This is sufficient, simpler and on top of everything—measurable.

In principle, a scheme as proposed by Bergmüller et al. (2007) can be useful to organize thoughts and research approaches. There are alternative ways to do this, and numerous details would be worth discussing about their particular outline, but I will confine my comments to an omission that I regard as particularly important. In their scheme, Bergmüller et al. omit the level of generalized reciprocity. This is important, because in their discussion of *N*-player cooperation, they propose that when “individuals invest into common goods, . . . theory predicts that cooperation should break down.” This is the traditional view highlighted by Robert Trivers (1971) 35 years ago, but in the meantime there has been research showing that generalized reciprocity, i.e. the help provided in response to help received from anyone else—can be evolutionarily stable (not only in spa-

tially structured populations, where group selection can take effect, and when population dynamics maintain cooperation, e.g. Hauert et al., 2006; Killingback et al., 2006; see Aviles, 2002; Hamilton and Taborsky, 2005a; Pfeiffer et al., 2005; Nowak and Roch, 2007; Rutte and Taborsky, 2007). This omission is important because generalized reciprocity is likely to affect the propensity to help at any level of sociality, including cooperative breeders. It is also inherent in the third of the “key questions” of Bergmüller et al. (2007).

4. Theories of cooperative breeding and the empirical approach

Bergmüller et al. (2007) selected pay-to-stay, group augmentation and prestige as major explanatory concepts of cooperative breeding. While I agree that these are powerful and adequate theoretical concept explaining cooperation in animal societies, I would propose to establish a more general framework. Cooperation that is not subject to kin selection can be explained at the evolutionary level by (1) reciprocity, which includes pay-to-stay and group augmentation as important mechanisms explaining cooperative breeding (e.g. Kokko et al., 2001, 2002; Hamilton and Taborsky, 2005b), (2) social prestige, which includes reputation mechanisms that have yet to be demonstrated to affect the evolution of cooperative breeding (see Lotem et al., 2003), and (3) forced cooperation, which is also unclear yet in the extent to which it affects cooperative behaviour in highly social animals (see West-Eberhard, 1975; Clutton-Brock and Parker, 1995; Tebbich et al., 1996; Gardner and West, 2004). To our present knowledge, the first of these explanatory concepts (reciprocity) is by far the most important to explain complex sociality, apart from kin selection. This more general framework might provide a more balanced and comprehensive outline to test the explanatory power of concepts that do not (or not necessarily) involve kin selection.

I support Bergmüller et al.'s (2007) lamentation that “empirical studies on cooperative breeding focus on ecological parameters and final net outcomes but usually not on the exchange of cooperative behaviours”. Even though I am not quite as pessimistic because there is already a number of studies on this very issue (e.g. Taborsky, 1985; Tebbich et al., 1996; Bergmüller and Taborsky, 2005; Cronin et al., 2005; Stiver et al., 2005; Kutsukake and Clutton-Brock, 2006), this aspect needs more attention. I also agree with the implicit idea that focusing more extensively on individual reactions and interactions in cooperative breeders will help to create a mutual interest between empirical research in this field and the development of general theoretical concepts to explain cooperation. If cooperatively breeding species – with all their complexity – are ideal test cases to investigate fundamental cooperation mechanisms has yet to be found out.

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