

Commentary

Despotic partner choice puts helpers under pressure?

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The authors of the target paper (Bergmüller et al., 2007) try to bring order into the many forms ‘cooperation’ takes in the natural world by designing a decision tree, most branches of which have endpoints well known from the cooperation literature. The advantage of this exercise is that it helps to classify natural phenomena into the correct pigeonhole and relate it to other natural phenomena of the same class as well as to existing theoretical considerations. The crucial assumption here is that a relatively small number of pigeonholes suffices to classify all observed cooperative phenomena. Otherwise, one has to create ever-smaller branches or accept that many phenomena get stuck between branches. For example, where do we classify the behaviour of a helper, who gains direct benefits through group augmentation (pseudo-reciprocity) plus indirect benefits through increased reputation (indirect reciprocity) and inclusive fitness?

One reason the tree presented in the target paper remains more or less orderly is that the authors have left out some important mechanisms, such as partner choice in general (see p. 14 of the Ms) and competitive altruism in particular (Barclay and Willer, 2007; Roberts, 1998), as well as restricted themselves to cooperative breeding. My impression is that the tree would become rather bushy without those restrictions and that we will run out of terms at some point. Pigeonholing can be very useful in ordering our thoughts about phenomena. The risk is that we artificially split up what is conceptually in fact identical or comparable. In my recent review for *Animal Behaviour* (Noë, 2006) I went the opposite direction and proposed to concentrate on two essential parameters: cooperative investment and cooperative returns. Both can come in many disguises, such as reproduction, protection, food, reputation, etc. and can be measured in relative fitness or in proximate currencies, such as risk of injury or gains and losses in time and energy. The puzzle then reduces to identifying the factors that determine the values of investments and

returns. Examples of such factors are the difference between participants in physical force or in the number of alternative options each has; the degree of kinship between them; the time lag between interactions, etc. In essence the question is what determines the amount of control each participant has over the investment (s)he makes and the returns (s)he obtains. The drawback of my approach is that one cannot always easily make the connection to existing theoretical considerations. Not that this is always a big loss, since some theoretical considerations out there lack all connection to empirical facts anyway. The advantage is that one can go down straight to the business of measuring and analysing the essentials in the particular system at hand rather than worrying over the correct label.

My more direct comments to issues brought up by Bergmüller et al.’s target paper concern the following themes:

- (1) The causes and consequences of power asymmetries between breeders and helpers.
- (2) Sociality as a cooperative investment.
- (3) The distinctions between three related phenomena: harassment, punishment and sanctioning.

1. Causes and consequences of power asymmetries between breeders and helpers

Bergmüller et al. (2007) chose not to include partner choice as one of the discriminating factors in their decision tree (p. 14 in the Ms). I assert, however, that this makes the exercise futile, because no helper system with more than one helper can be understood without considering the consequences of partner choice. Through partner choice breeders can in principle play off their own offspring and other underlings against each other. This changes the power balance and thus the investments done by both parties.

In my explanation I largely repeat a story published quite a while ago (Noë et al., 1991). I restrict myself here to a verbal argument based on a situation in which there is one breeding pair

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with two or more helpers that are unrelated to them. The main consequences of excluding kinship effects are that (a) the breeders have no interest in the reproductive success of the helpers, neither as dispersers nor as heirs of their breeding positions and (b) the helpers do not increase their inclusive fitness by helping. I further assume that (1) Helpers can provide benefits to breeders in only two forms: provisioning of the young and increasing safety (dilution; early warning, etc.). (2) Helpers benefit through the safety of group living and access to the resources in the group's territory. I ignore eventual future benefits returned by the offspring the helpers care for, because it is difficult to see how helpers could control reimbursements in this form. Note, however, that examples of such 'delayed reciprocity' have been reported (Ligon and Ligon, 1978, 1983). (3) The breeders are dominant over all other group members and present a common front, i.e. I ignore eventual conflicts of interest between breeders. I will use the term 'subordinate' for all adults other than the breeders in a cooperatively breeding group and the term 'helper' only for those subordinates that provision the breeders' offspring.

The following questions can then be asked:

- Can and do breeders force helpers to help more than they would do voluntarily?

I consider it very unlikely that a cooperative breeding group is without conflicts of interests and assume the most likely situation here, namely that helpers tend to help less than is optimal from the point of view of the breeder. A tell-tale sign of a power asymmetry between breeders and helpers is that breeders reduce their own effort more when there are more helpers (for a classical example see Brown et al., 1978). This assumption of a power asymmetry is the basis of any 'paying-for-staying' explanation (Gaston, 1978) as well as skew models of cooperative breeding (Kokko et al., 2002). In an egalitarian society all members would reduce their effort equally if the total effort suffices to feed the young. Kin selection can mask power struggles, however. Breeders and helpers have been found to work equally hard in highly related breeding groups (e.g. Wright, 1997) or breeders may even work harder than their helpers in such groups (e.g. Woxvold et al., 2006).

How can breeders gain leverage over subordinates? I can think of three options: (1) blocking their attempts to reproduce, (2) punishment and (3) denying them access to vital resources. With punishment I refer to aggressive behaviour resulting in a change of the future behaviour of the punished to the benefit of the punisher (see also last section below). Denying access to vital resources could be temporary (e.g. to a safe nest or food supplies) or permanently (e.g. expulsion from a territory). The former boils down to punishment when the term is used in a broad sense. Expulsion and permanent exclusion of vital resources go in the direction of 'sanctioning' (see below). I do not think 'harassment' will play a major role, but I could see a breeding bird occasionally chasing around a reluctant helpers with a bundle of worms in its mouth till the helper delivers them in the nest (see Noë, 2006 and below for a discussion of the term harassment). Mulder and Langmore

(1993) provide experimental evidence of punishment (or even harassment?) of helpers that had been removed from the group for 24 h and could thus have been perceived by breeders as helpers that had made themselves scarce.

- When do breeders use force and against whom?

Kokko et al. (2002) used reproductive skew theory to model cooperative breeding. They also assumed a power asymmetry between breeders and subordinates, as I do here, but their model is based on a single breeder with a single helper. This leaves an essential question out of consideration: what happens if there are two or more (potential) helpers? The answer is that partner choice by the breeder is inevitable. Breeders would not be able to put equal pressure on their subordinates, because of simple physical constraints, even if they would want to. Simply put: it is hard to chase around two subordinates simultaneously. Label lovers might want to call this form of negative partner choice 'despotic partner choice'.

Breeders will be choosy for other reasons than such constraints. Negative choice implies punishment and other forms of coercion of helpers are costly to breeders. Breeders should make such investments in the most economical way possible. They stand to gain most when they invest most in punishing the helper from which most improvement can be expected. Normally speaking this is the 'laziest' helper. If breeders evict helpers, they should also start with the least profitable one.

Bergmüller et al. (2007, p. 14 of the Ms) discuss partner choice, but talk about breeders choosing 'other helpers' (i.e. 'positive' partner choice) and helpers 'switching breeders'. I bet that those cases are exceptions rather than the rule and that the most common form of partner choice is despotic and negative. Helpers will probably only switch breeders in species in which kinship plays no role in the helpers' strategic choices (see also below under 'Can and do helpers adjust their effort.').

In any case, partner choice turns cooperative breeding populations into 'biological markets' (Bshary and Noë, 2003; Noë, 2001; Noë and Hammerstein, 1994, 1995). Thus, my *conjecture*: a cooperative breeding system functions as a biological market when there is (a) more than one helper, (b) a conflict over investment between helpers and breeders and (c) a power asymmetry between helpers and breeders. Looking at cooperative breeding in the light of the biological market paradigm suggests a few more interesting questions:

- How do helper numbers influence power asymmetries?

This question addresses two points that are typically considered in the light of the biological market paradigm: what is the exchange rate between the commodities offered by two partners and how does each party arrive at obtaining the best possible rate?

Consider a system in which a breeder can permanently exclude subordinates from crucial resources, e.g. deny them access to a communal den or expel them from a territory. The time to throw out a subordinate has come when the cost of accepting his presence are higher than the costs of exclusion. Subordinates can be costly, for example, due to scramble competition with the breeder and his family. The more subordinates there are, the more likely this point is reached for at least one of them. This is also true when all subordinates

help, assuming that the total benefit from helpers reaches an asymptote with increasing numbers of helpers, as is often the case (see contributions in: Solomon and French, 1997; Stacey and Koenig, 1990). From the point of view of a subordinate, the time for leaving has come when the limitations of access to the crucial resource plus the burden of aggression by the helpers exceeds the costs of dispersal. In any case, the more helpers, the lower the value of each helper for the breeder and the higher the power asymmetry between helper and breeder. For systems in which older offspring take care of their younger sibs, this could put a positive feedback loop in motion: the more helpers and the harder they work, the more offspring; the more offspring, the more helpers in the next round; the more helpers, the higher the power asymmetry and the harder they work. This feedback loop may even set a second one in motion, namely between population density, habitat saturation and helping (see Kokko et al., 2002, for a similar argument).

The power asymmetry between breeders and helpers can be counter-balanced if subordinates manage to form effective coalitions against breeders. However, it is more likely that coalitions are formed against subordinates by other subordinates or between breeders and subordinates. The power asymmetry improves in favour of the remaining subordinates with each competitor removed. *Conjectures*: (1) The better the control of breeders (i.e. dominants) over crucial resources, the harder helpers work. (2) The relative contribution per helper increases with the number of (unrelated) helpers, but the relative contribution of breeders decreases. The decrease in breeder contribution has been found in several studies already (e.g. Brown et al., 1978). A market effect was shown for unrelated helpers in pied kingfishers by Reyer (1986, 1984); see also Noë et al., 1991), but this may be the only example of its kind (Wright, 1997).

- Can breeders base their choice among helpers on the helpers' relative contributions?

Breeders that put physical pressure on their helpers will have to choose which helper to punish or to exclude first, as stated above. They will invest in aggression considerably more efficiently when they can discriminate on the basis of profitability, or even better, on the potential of increasing profitability. Measuring the effort of a helper is no simple matter, however. Behavioural ecologists often need cameras and scales to get an idea how much each caretaker delivers in the nest or den. Many breeders will have to rely on proxies, such as the number of visits and the effect of the visit on the begging behaviour of the young. They can obtain this information only when they are present at the nest or den themselves. A similar point has been raised in connection to helping as a 'honest signal', which also works only if bystanders witness the act of helping (Wright, 1997). Thus, possibly there is another positive feedback loop: with more and more effective helpers, breeders have to work less hard themselves and can thus control their helpers better. There is ample scope for 'subtle cheating', however (bringing small prey, swallowing food with the head already in the nest hole, etc. (see Wright, 1997, among others)). *Conjecture*: the bet-

ter breeders can judge the 'productivity' of their helpers, the stronger the effect of partner choice will be.

- Can and do helpers adjust their effort to the contributions of other helpers?

In order to avoid being targeted by the breeders, a helper should help more than his competitors, i.e. the other helpers (Noë et al., 1991). Roberts' 'competitive altruism' is based on the same idea. He proposes that "*individuals can make a strategic decision about how much of their available resources to invest in altruism*" (Roberts, 1998 p. 428). This rests on the assumption that those competing altruists have a way of knowing when they do enough to out-compete the others. But, helpers have the same information problem that breeders have: how can they measure the effort of other helpers? How would they know what others bring to a nest when they are making a foraging trip themselves? At evolutionary time scales I see little problem. Market selection driven by partner choice can work just like sexual selection driven by mate choice (Noë, 2001): over the generations the amount of investment adapts to the prevailing market situation. When supply always outstrips demand in a specific species, then helpers are always forced to provide maximum effort. Helping becomes a peacock's tail and helping effort becomes not only an honest signal of altruistic attitude (Zahavi, 1995), but also of general quality, e.g. as a future mate (cf. Hawkes and Bliege Bird, 2002).

However, we are talking here about adjustments of helping efforts within the breeding season. The economics compare to those of small enterprises with a few employees, such as a farm or a garage. Verbal arguments would not carry very far, but I can try to think about what happens at the extreme ends of employee numbers. For a garage owner it doesn't make much sense to stop repairing cars himself, to pay a salary of a car mechanic and to spend all available time supervising him. The owner's income increases only when the mechanic increases the total production of the garage by working alongside the owner. It may pay to specialise more in supervising, however, with an increasing number of employees. Much depends on how easy it is to control the employees' output, i.e. gathering information about their efforts, and forcing them to work harder. The mere threat of sacking will do the job with a lot of unemployed mechanics on the market and a hiring and firing system with little friction. Likewise, breeders have to find the right balance between the effort they put in provisioning the young themselves and in supervising provisioning by helpers. If there are many helpers and/or helpers are easily replaced, they can put almost all effort in supervision. These would be the systems in which the breeders reduce their own effort progressively with more helpers available. Helpers in such cases will put in maximum effort unless they can escape scrutiny by subtle cheating. Each helper has to take care that the breeder is aware of its effort in order to avoid being singled out as the least profitable helper. One can therefore predict that helpers under competitive pressure are sensitive to the signalling function of their effort and provide nestlings preferably in the presence of breeders.

If, on the other hand, helpers are rare, breeders can only force them to do enough to compensate for their use of scarce resources. Here systems with unrelated helpers may differ from systems with related helpers in a crucial way: unrelated helpers could exert choice themselves by switching breeding groups, as suggested by Bergmüller et al. (2007). Most related helpers would have a single breeding group in which their inclusive fitness is maximised for the same investment.

There seems to be a tendency in the cooperative breeding literature to equate time and energy invested by helpers directly by time and energy gained by breeders. This equation seems too simple to me, however, because I cannot imagine that helpers work very hard if breeders do not invest (1) in gathering information about their helpers' investment, which translates in limits to their own foraging options, and (2) in putting pressure on the helpers, which translates in investments in time and energy and eventually in increased risk.

- What is the role of information about investments and outside options?

What happens in between extremes in helpers/employee numbers depends for a good part on the quality of information. In the following I only consider information flows within the breeding unit. Note, however, that it is also important to consider information about the population-wide market. There could be an important asymmetry here, because breeders can stay put and helpers have to move around to gather information on breeding opportunities and vacancies for helpers. If information on helper effort is complete for helpers and breeders, then both parties can adjust their investments accurately. With relatively few helpers, breeders cannot risk losing them by pushing too hard, but they can target the laziest helper while leaving others alone even at small differences. Helpers cannot afford to work less than their fellow helpers when their numbers are relatively high, but on the basis of good information they can adjust their effort accurately to match the others. I guess that in either case all helpers within a group will pay a price that is close to the exchange ratio dictated by the market situation. In contrast, I conjecture that the system will tend to flip from one extreme to the other if information on helper contributions is hard to come by. A breeder with many helpers may take the risk of putting considerable effort in gathering information and punishing the laziest helpers, thus forcing them either to quit or to work harder. If few helpers remain, the breeder will have to work harder on provisioning and loose control over his helpers. This will cause them to work less and thus the breeder will be forced to invest even more in provisioning. I am more than willing to admit that my guesses are wrong if someone produces a sound ESS analysis of cooperative breeding systems with varying levels of information. I risk one prediction: unrelated helpers will be either hard working or lazy with little in between. In species with related helpers this will be dampened either way because breeders have a genetic stake in their helpers and the helpers in the young they provision.

2. Group living as a form of cooperation

At several points Bergmüller et al. (2007) suggest that group living is a form of cooperation that requires no investment, but provides benefits to the participants. On p. 3 for example the benefits of group living are described as by-products of the presence of conspecifics. I think some prudence is called for. It is hard to see how an individual can live in a group without compromising its optimal foraging and reproduction strategies for the sake of staying together. It is unlikely that foraging routes and patch stay times are identical for all individual group members or age-sex classes involved. Coordination of movement itself carries some cost (Conradt and Roper, 2005). All but the highest ranking members suffer from contest competition and those high-ranking individuals still suffer from scramble competition. The cost of group living is reflected in the large brain size that is apparently needed to handle it (Dunbar, 1995; Dunbar and Bever, 1998; but see Iwaniuk and Arnold, 2004). Of course animals would not live in groups if there would be no compensation, but as with all other forms of cooperation is worthwhile to separate the investments from the returns and to do so for each individual separately. Group living is not the most intriguing form of cooperation from a theoretical point of view, because some returns are immediate and largely guaranteed, e.g. protection against predation due to dilution. Conflicts over investments and returns in this arena have given rise to a large literature, however. The fact that in most of these papers group living is not likened to cooperation does not mean that it does not fall under the prevailing definitions of cooperation, among which those used by Bergmüller et al. (2007).

3. Harassment, punishment and sanctioning

Is 'harassment' a useful label for a specific phenomenon relevant to our understanding of cooperation? Consider two scenes from the life of monkeys. *Scene 1*: Monkey A eats from a bush with berries; monkey B approaches and hits A over the head; A accepts that B starts eating from the bush too. *Scene 2*: Same A eating from same bush; infant monkey C approaches and starts screaming its head off, which is likely to attract support from C's mother, who is dominant over A; A does not wait for this to happen and accepts that C eats berries too. If you see a fundamental difference between these two scenes, then you probably need the term 'harassment' to describe scene 2. The term is not mentioned by Bergmüller et al. (2007), in contrast to 'punishment', which occurs many times, and 'sanctioning', which occurs twice. All three terms have been used in connection to cooperation and I think it is useful to clarify them and eventually give each of them a separate role. In biology, phenomena are rarely completely and clearly separated, so some overlap should be tolerated in practise. For theoretical purposes we can give clear-cut definitions, however. Here is my proposal (see also Noë, 2006):

- *Harassment*: Individual X behaves in such a way that individual Y is forced to act in a manner beneficial to X within a single uninterrupted interaction, i.e. X only stops when Y capitulates. Important point: the benefit for X is immediate

and thus the risk of investing with no returns is low. It only makes sense to use the term harassment when *Y* is forced to *act* in some way beneficial to *X*. Otherwise the interaction can be described as stealing, predation, parasitism, etc. A borderline case would be a gull dropping food (act: opening its bill) while being chased by a skua, an interaction usually labelled klepto-parasitism. A core example of cooperation under harassment is described in Tebbich et al. (1996). If I follow the decision tree in Figure 1 of Bergmüller et al. (2007), I arrive at ‘direct reciprocity’ (investment-yes; costly response-yes; investor receives direct benefits). I wonder whether the authors consider the interaction of Tebbich et al.’s keas a good example of direct reciprocity, however.

- **Punishment:** *X* behaves in a way that is harmful to *Y* after perceiving a failure of *Y* to act in *X*’s favour. Punishment works if it increases the chance that *Y* acts to the benefit of *X* in the future. Technically speaking *X* uses negative reinforcement to shape *Y*’s behaviour. A nice example is described in Bshary and Grutter (2005). The time lag between the punishment and the beneficial act decreases the control by *X* and thus increases the risk of no returns. In Box 1 Bergmüller et al. (2007) follow Clutton-Brock and Parker (1995) and use the term ‘negative reciprocity’ as an alternative to ‘punishment’. In this terminology ‘positive reciprocity’ is equivalent to reciprocal altruism (Trivers, 1971), stressing the importance of the time lag between investments and returns in both cases. The examples given by Clutton-Brock and Parker suggest a less clear-cut definition than I just gave by also including instances that I would label ‘harassment’. Bergmüller et al. (2007) also equate all “fitness reducing actions” with punishment (see their abstract). Putting less stress on time lags and considering them as but one of several sources of loss of control (Noë, 2006) is consistent with the authors’ decision not to make a fundamental distinction between ‘simultaneous altruism’ and ‘reciprocal altruism’ (p. 6 of target Ms). I am in favour of using a single term for all forms of ‘positive reciprocity’ and another for all forms of ‘negative reciprocity’, but I would prefer using the verbs ‘cooperate’ and ‘punish’ to make unambiguously clear that we talk about individual strategic choices rather than outcomes of interactions.
- **Sanctioning:** After experiencing insufficient benefit from its interaction(s) with *Y*, *X* not only ends his relationship with *Y*, but *de facto* ends *Y*’s existence. This mechanism plays a role notably in mutualisms in which a single large partner interacts with many small ones, e.g. a plant interacting with rhizobia or with mycorrhizal fungi, or a yucca interacting with yucca-moths (reviewed in: Bronstein, 2003; Bshary and Bronstein, 2004; Sachs et al., 2004). In contrast to punishment, sanctioning does not shape *Y*’s future behaviour, but has a selective effect on the gene pool of the population to which *Y* belongs. In Box 1 Bergmüller et al. (2007) propose the alternative label ‘negative pseudo-reciprocity’, because the demise of *Y* is a direct consequence of a selfish act of *X*, namely ending an unprofitable relationship. While this will apply in many cases, it doesn’t apply in all. *X* can discriminate between *Y*’s by ‘sanctioning’ the least productive *Y*’s although all contribute to *X*’s fitness in a positive way. This

would still be sanctioning, but not pseudo-reciprocity. For an enlightening example see Kiers et al. (2006).

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