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Commentary

Cooperative behaviour and cooperative breeding: What constitutes an explanation?

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We all have experienced the proliferation of electronic access to manuscripts and various Internet-based search tools for scientific literature. Nevertheless, it remains a tall order for a scientist to find all relevant information that will advance his or her thinking on a subject. Sometimes the lack of communication can be blamed on different terminology or even geographic distance (Wong and Kokko, 2005), but regardless of the obstacles that need to be overcome, one should avoid reinventing the wheel or progressing in different directions when common themes exist. Unfortunately, examples of taxon-myopic or otherwise unnecessarily constrained thinking are abundant. Already while studying lekking behaviour for my PhD, I was struck by how rarely papers on lekking birds cited any literature on lekking mammals, and vice versa. Limitations of web-based searches certainly cannot be the blame when the same keywords appear in both fields. Likewise, there is no excuse for a lack of information flow between people studying cooperative behaviours and those who focus on cooperative breeding. Yet, despite the fact that to a layman the terms sound almost identical, Bergmüller et al. (2007) show that the study of these two fields has proceeded almost completely separately.

Perhaps such a gap is what is expected wherever theoreticians and empiricists try to meet. In the theory-dominated cooperative behaviour literature, empirical examples sometimes appear almost anecdotal or, to be more fair, they concentrate on a few model organisms. The topic of cooperative breeding, on the other hand, is strongly driven by field studies of a great diversity of organisms (although again, the efforts of theoreticians in this area should not be neglected). Thus, the unifying efforts by Bergmüller et al. (2007) should be extremely valuable. It is indeed curious to note that terminological clarification seems to be the current topic in these two interrelated fields: this year has seen a thorough terminological review by West et al. (2007) that re-evaluates the usage of plenty of terms used in social evolution, and a 'target review' by Lehmann and Keller (2006) that sought to categorize all cooperative behaviours using a comprehensive framework and attracted no fewer than 15 responses.

The three papers taken together (Lehmann and Keller, 2006; West et al., 2007; Bergmüller et al., 2007) should provide much food for thought and help clarify misunderstandings. Still, it is telling that differences remain. For example, 'cooperation' in West et al.'s definition differs from that used by Bergmüller et al. (2007) in that it adds the requirement that the behaviour is selected for because of its beneficial effect on the recipient (thus excluding byproduct mutualism). Even though Bergmüller et al. (2007) do not explicitly define cooperation in this way, the sense in which they use cooperation has evidence of similar implicit thinking: immediately after presenting a definition they proceed to consider that cooperation can be either selfish (directly selected) or 'seemingly' altruistic. These formulations clearly hint at the need to explain the adaptive value of each cooperative behaviour in order to be classified as such. But later they also seem to include byproduct mutualism as a maintenance mechanism for one causal route to cooperation ('passive' group augmentation), which may create misunderstanding (I shall return to this question in detail below). Further, it is clearly not an ideal situation to first restrict the use of mutualism to interspecific interactions and then have to make an exception with byproduct mutualism, and West et al.'s (2007) suggestion to simplify the terminology by talking about 'mutual benefits' appears more sensible. In general, it appears that the field has not yet rid itself of subtle and potentially confusing terminological differences, and consequently one almost wishes someone would

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write a 'meta-review' of Bergmüller et al. (2007), Lehmann and Keller (2006), and West et al. (2007).

1. What is an explanation?

What are we aiming at when we try to explain a behaviour? Many empirically oriented students are highly likely to find abstract phrases such as 'negative pseudo-reciprocity' less friendly to grasp than a catchy phrase such as 'pay to stay'. Friendliness of course is not the best criterion for good science, so it is worth reflecting for a moment on what constitutes a potential explanation, in other words a hypothesis. The value of the approach of Bergmüller et al. (2007) is that they show how many explanations from the realm of cooperative breeding are 'compound' hypotheses, in the sense that they often make use of several mechanical components that in turn have been amply studied by theoreticians. The compound hypotheses of cooperative breeding can be seen as 'higher-level' explanations, in that they typically aim at measuring lifetime inclusive fitness. Cooperation theory, on the other hand, typically focuses on 'lower-level' building blocks such as short-term payoffs from behavioural encounters. But should one level of explanation be favoured over the other?

Undoubtedly, questions are relevant at both levels. If theory showed that, say, negative pseudo-reciprocity was for some reason very problematic, then any higher-level explanation that makes use of negative pseudo-reciprocity should take such results seriously. This amply justifies Bergmüller et al.'s (2007) call to pay more attention to both levels. At the same time, it remains a useful question to ask how often all the components of a succinctly phrased hypothesis such as 'pay-to-stay' can be fulfilled simultaneously in a real organism in its ecological setting. The framework proposed by Bergmüller et al. (2007) will indeed be most useful if used for this purpose; it would therefore be beneficial if each of the arrows in their schematic figures was followed by an evaluation of how easily this route leads to behaviours that appear cooperative, what ecological conditions might promote this particular route, and whether such conditions are common.

At the same time, one should be cautious not to fit the higher-level arguments to the low-level mechanisms too forcefully. Bergmüller et al. (2007) suggest, for instance, that the division between passive and active group augmentation equals that between byproduct mutualism and pseudo-reciprocity. However, this may reflect a forced attempt to make boundaries match between different levels of explanation. Passive group augmentation is a mechanism in which costly alloparenting (or some other form of cooperation) is selected for because an individual benefits by living in a larger group in the future. The 'passivity' refers to the fact that the correlation between group size and a future fitness component exists irrespective of whether the newly produced offspring behave cooperatively themselves (if they do, one shifts to the realm of 'active' group augmentation). Importantly, the 'passivity' does not mean that there was no investment involved by the alloparenting individual: instead, the passively existing correlation can be sufficient to create selection for a true investment that trades off with the individual's current survival (Kokko et al., 2001). Thus, passive group augmentation differs from Bergmüller et al.'s (2007) byproduct mutualism in that only the former is true cooperation according to the strict criterion of West et al. (2007), and the assertion by Bergmüller et al. (2007) that no investment is involved is inconsistent with the original definition of passive augmentation.

The point that some higher-level explanations do not fall easily into single categories was, in the same context of group augmentation, also raised by West et al. (2007). It is therefore advisable that the charts provided by Bergmüller et al. (2007) will be used with caution, to avoid the pitfall of thinking along predefined paths where reality is more complex. An interesting topic for further research is to document how often augmentation benefits are passive only, or whether they rely on an active component. The difference is not the presence of current investment, but whether the newly raised offspring return enough active help later in life to form a significant causal explanation of alloparenting, in addition to any 'passive' correlations present. In fact, if most individuals engage in cooperative behaviours in the groups that they live in, it could turn out to be harder to find examples that are strictly restricted to passive benefits only, than ones in which individuals can to some extent rely on actively returned help too. This said, I agree with Bergmüller et al. (2007) that solid evidence is lacking so far.

2. What is the question?

It appears that there are two separate questions when explaining cooperation and cooperative behaviour: (1) what mechanisms exist that can promote cooperation and what are the requirements for each to operate, and (2) what ecological conditions favour suitable parameter values that allow for the said requirements to be fulfilled. To some extent, this division reflects the respective research foci in the study of cooperation vs. cooperative breeding. However, with all due respect to the difficulties posed by real-life field studies, it appears that the second question is further from a definitive answer than the first, lower-level question. A crucial test of whether satisfactory answers have been obtained to both questions is whether we can assess the relative importance of each of the proposed mechanisms to the extent that we can predict the global distribution of species in which cooperation occurs.

There is little use in stating, for example, that tighter ecological constraints promote cooperation within a species, when numerous non-cooperative species exist with apparently equally difficult prospects for young breeders to establish themselves (Hatchwell and Komdeur, 2000; Ekman et al., 2004). Likewise, stating that kin selection underlies much of cooperation is an empty statement unless variation between species can be explained: individuals are related to their relatives in all species (a tautology), yet only certain species breed cooperatively. This is the principal reason why the study of Hamilton's rule ($br > c$) to explain invertebrate sociality has experienced a shifting emphasis from a focus on relatedness r to quantifying benefits b and costs c (e.g. Wenseleers et al., 2004; Queller, 2006; Wenseleers and Ratnieks, 2006); importantly, this does not imply that kin selection has suddenly become unimportant (for a recent debate see Fletcher et al., 2006; Foster et al., 2006a,b). Note also that it remains true that unusual inheritance rules such as haplodiploidy can influence the rules of how resources are put into use to aid the spread of relatives' genes (Teyssèdre et al., 2006).

3. What is the solution?

When ecology is taken into account, several ideas emerge that extend the scheme of Bergmüller et al. (2007). Imagine a set of parameter values that influences how likely one follows one or another arrow in Bergmüller et al.'s (2007) figures: for example, how easily individuals can coerce others to stay, or how easy it is for them to use public information. There are several ways for the distribution of such parameter values to become non-random and thus potentially help to explain which path species end up following:

1. *Phylogenetic constraints*. Constraints on evolutionary change have the potential to make certain parameter values appear repeatedly in a species tree. Cooperation is indeed distributed unevenly; for example, a phylogeny of oscine passerines suggests that cooperation implies low speciation rates and low capacity to cross large geographic distances (Cockburn, 2003). This pattern has been argued to reflect the fact that pair-breeding species have more mobile habits as their offspring disperse, and cooperation is also difficult to maintain in species with migratory habits (Cockburn, 2003, see also Baglione et al., 2005). To what extent phylogenetic inertia can explain cooperation is perhaps best regarded an open question. In a phylogeny of corvids, the trait appears rather labile, readily responding to environmental challenges (Ekman and Ericson, 2006), whereas the debate on invertebrate eusociality has even brought up phrases such as "irreversible contingency" (Maynard Smith and Szathmary, 1995) or "point of no return" (Wilson and Hölldobler, 2005) after which species can only exist if they keep to their eusocial lifestyle with morphologically differentiated workers. Many of the mechanisms proposed by Bergmüller et al. (2007) depend on traits such as cognitive abilities, which almost certainly can have a very strong phylogenetic component, thus at least the potential for significant phylogenetic inertia should always be taken into account.
2. *Coevolution of the decision to stay and the decision to help*. Bergmüller et al. (2007) correctly state that the decision to stay is not the same as the decision to help. However, the distinctness of the two decisions should not be overemphasized, if it leads to the impression that helping interactions can be sufficiently characterized as a two- or *N*-player game with the number of players fixed. Bergmüller et al. (2007) themselves emphasize the importance of biological markets and outside options, which in the real world means that the evolution of cooperative interactions within a group and the tendencies to leave a group become linked. The two decisions may be independent in principle, but the selective pressures acting on them are not, and hence we can expect coevolution to occur.

   There is indeed an emerging body of theoretical work on coevolution of dispersal and cooperation that empiricists could take better note of (e.g. Aktipis, 2004; Hamilton and Taborsky, 2005; Le Galliard et al., 2005). When cooperative behaviour and dispersal coevolve, the diversity of outcomes is much richer than expected by investigation of either alone, including a counterintuitive possibility that more mobile organisms can display higher levels of cooperation in comparisons across species (Le Galliard et al., 2005). It would obviously be fruitful to link such results to the details of partner choice, which is a somewhat finer-scaled problem focused on by Bergmüller et al. (2007).
3. *Life histories and population-level feedback*. This concept is related to the previous one on coevolution, and relies on the fact that parameters such as 'ecological constraints' are not fixed for each species but are emergent traits that evolve with the population. As repeatedly pointed out by Jan Ekman and coworkers, a tight constraint on independent breeding does not dictate philopatry. It simply dictates that an offspring has to wait, without specifying where (e.g. Ekman et al., 2001, 2004). Only once one knows how prospects of survival and breeding vary across different habitats or territories, one can predict what young individuals should do: stay or leave, and in either case, be more or less helpful towards conspecifics.

   Currently, there is an apparent mismatch between experimental results that find more dispersal when new breeding opportunities arise (e.g. Komdeur et al., 1995) or resources at home are diminished (e.g. Dickinson and McGowan, 2005), and the observation that across species, habitat saturation does not appear to explain much of the occurrence of cooperative breeding (Hatchwell and Komdeur, 2000). Moreover, the support for the role of life history as a determinant of cooperative habits appears mixed (e.g. Arnold and Owens, 1999; Ligon and Burt, 2004; Doerr and Doerr, 2006). Many apparent contradictions could potentially be resolved if the problem was tied back to the way how population structure and density emerge from patterns of individual breeding success and survival. For example, it makes sense that individuals disperse from locally crowded conditions, or from locally poor sites. But if all habitat is made uniformly crowded (or of uniform quality), as is the case when a species evolves to have a life history that predicts high density, then moving between sites may yield little improvement for most individuals. This is why experiments that investigate individually plastic responses to local changes (e.g. Dickinson and McGowan, 2005), while useful to detect patterns of within-species plasticity, do not always scale up to a species-level comparison (Kokko and Lundberg, 2001).

   Instead, true predictions can be generated if the full life cycle is considered: a life history pattern together with assumptions on habitat availability can be used to calculate how likely a disperser secures a breeding location of a given quality. This calculation must be self-consistent such that it accounts for the number of other dispersers and competing philopatric individuals in the population, which in turn depends on breeder productivity across habitats (Pen and Weissing, 2000; Kokko and Lundberg, 2001; Kokko and

Ekman, 2002). This way one can predict, for instance, that the relative advantage gained by staying at home based on parental favouritism (which exists irrespective of overall density) may matter more than how generally tight competition is in the environment (Kokko and Ekman, 2002).

The bad news is that when several factors are considered simultaneously together with feedback among them, predictions are rarely as clear as when artificially fixing some parameters such as 'constraints'. But if life history truly influences the frequency with which vacancies arise and the ease of filling them, then this link must be included before realistic predictions can be made (Kokko and López-Sepulcre, 2007). It is highly likely that theory has not yet explored every possible co-occurring direction of causality (feedback): for example, low mortality may favour certain behaviours but beneficial group behaviours can in turn lower the mortality of its members (Krause and Ruxton, 2002; Ligon and Burt, 2004). For the scheme proposed by Bergmüller et al. (2007), it is promising indeed that some of the most recent ideas link aspects of life history back to the lower-level processes considered by Bergmüller et al. (2007): as an example, a long lifespan may be a prerequisite for repeated social interactions, which again are essential for the evolution of reciprocity (Ridley et al., 2005).

4 *Multi-level selection*. The phrase 'group selection' often evokes shudder and frowning among evolutionary biologists, yet when properly applied it is mathematically equivalent to kin selection (Queller, 1992; Foster et al., 2006b). Important selective effects can even be expected to occur at scales above single social groups, such as populations or species. In the social amoeba *Dictyostelium discoideum*, single-cell organisms group to form multicellular reproductive structures in which cells that form the stalk will altruistically die. Foster et al. (2004) showed that 'cheater' genotypes (that avoid participating in pre-stalk formation) could not proliferate because of pleiotropic effects that halt their success before reproduction can take place. In myxobacteria, artificially created 'cheater' strains were observed to cause extinction of whole populations, which might explain the absence of such cheaters in nature (Fiegna and Velicer, 2003). Foster (2006) has thus suggested that higher-level selection should be considered seriously in the evolution of cooperation and cooperative breeding: perhaps extant genetic architectures, or social systems in general, are those that possess enough robustness that they can resist at least the most commonly occurring attempts to cheat the system (Rankin et al., 2007). Empirical test of this idea remain obviously challenging (see Rankin and López-Sepulcre, 2005), but these studies repeat the theme of Bergmüller et al. (2007) that researchers interested in social evolution should pay more attention to studies that use different terminology, or are conducted on different taxa than their own.

4. Conclusions

The categorization of Bergmüller et al. (2007) highlights the distinction between lower and higher levels of explanation, and the need to unify them. The challenge does not stop there, however, before species-level patterns are fully integrated into the picture. The scheme of Bergmüller et al. (2007) is indeed a first step in this direction, hopefully leading to an assessment of the prevalence and strength of all the different mechanisms involved in various taxonomic groups and in different ecological or life history settings.

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References

Aktipis, C.A., 2004. Knowing when to walk away: contingent movement and the evolution of cooperation. J. Theor. Biol. 231, 249–260.

Arnold, K.E., Owens, I.P.F., 1999. Cooperative breeding in birds: the role of ecology. Behav. Ecol. 10, 465–471.

Baglione, V., Marcos, J.M., Canestrani, D., Griesser, M., Andreotti, G., Bardini, C., Bogliani, G., 2005. Does year-round territoriality rather than habitat saturation explain delayed natal dispersal and cooperative breeding in the carrion crow? J. Anim. Ecol. 74, 842–851.

Bergmüller, R., Johnstone, R., Russell, A., Bshary, R., 2007. Integrating cooperative breeding into theoretical concepts of cooperation. Behav. Processes 76, 61–72.

Cockburn, A., 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? Proc. R. Soc. Lond. B 270, 2207–2214.

Dickinson, J.L., McGowan, A., 2005. Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. Proc. R. Soc. Lond. B 272, 2423–2428.

Doerr, E.D., Doerr, V.A.J., 2006. Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. Anim. Behav. 72, 147–159.

Ekman, J., Ericson, P.G.P., 2006. Out of Gondwanaland: the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies. Proc. R. Soc. Lond. B 273, 1117–1125.

Ekman, J., Baglione, V., Eggers, S., Griesser, M., 2001. Delayed dispersal: living under the reign of nepotistic parents. Auk 118, 1–10.

Ekman, J., Dickinson, J.L., Hatchwell, B.J., Griesser, M., 2004. Delayed dispersal. In: Koenig, W.D., Dickinson, J.L. (Eds.), Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, pp. 35–47.

Fiegna, F., Velicer, G.J., 2003. Competitive fates of bacterial social parasites: persistence and self-induced extinction of *Myxococcus xanthus* cheaters. Proc. R. Soc. Lond. B 270, 1527–1534.

Fletcher, J.A., Zwick, M., Doebeli, M., Wilson, D.S., 2006. What's wrong with inclusive fitness? Trends Ecol. Evol. 21, 597–598.

Foster, K.R., 2006. Balancing synthesis with pluralism in sociobiology. J. Evol. Biol. 19, 1394–1396.

Foster, K.R., Shaulsky, G., Strassmann, J.E., Queller, D.C., Thompson, C.R.L., 2004. Pleiotropy as a mechanism to stabilize cooperation. Nature 431, 693–696.

Foster, K.R., Wenseleers, T., Ratnieks, F.L.W., 2006a. Kin selection is the key to altruism. Trends Ecol. Evol. 21, 57–60.

Foster, K.R., Wenseleers, T., Ratnieks, F.L.W., Queller, D.C., 2006b. There is nothing wrong with inclusive fitness. Trends Ecol. Evol. 21, 599–600.

Hamilton, I.M., Taborsky, M., 2005. Contingent movement and cooperation evolve under generalized reciprocity. Proc. R. Soc. Lond. B 272, 2259–2267.

Hatchwell, B.J., Komdeur, J., 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. Anim. Behav. 59, 1079–1086.

Kokko, H., Ekman, J., 2002. Delayed dispersal as a route to breeding: territorial inheritance 'safe havens' and ecological constraints. Am. Nat. 160, 468–484.

Kokko, H., López-Sepulcre, A, 2007. The ecogenetic link between demography and evolution: can we bridge the gap between theory and data? Ecol. Lett. in press.

Kokko, H., Lundberg, P., 2001. Dispersal, migration and offspring retention in saturated habitats. Am. Nat. 157, 188–202.

Kokko, H., Johnstone, R.A., Clutton-Brock, T.H., 2001. The evolution of cooperative breeding through group augmentation. Proc. R. Soc. Lond. B 268, 187–196.

Komdeur, J., Huffstadt, A., Prast, W., Castle, G., Mileto, R., Wattel, J., 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. Anim. Behav. 49, 695–708.

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press, Oxford.

Le Galliard, J.-F., Ferrière, R., Dieckmann, U., 2005. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. Am. Nat. 165, 206–224.

Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism: a general framework and a classification of models. J. Evol. Biol. 19, 1365–1376.

Ligon, J.D., Burt, D.B., 2004. Evolutionary origins. In: Koenig, W.D., Dickinson, J.L. (Eds.), Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, pp. 5–34.

Maynard Smith, J., Szathmary, E., 1995. The Major Transitions in Evolution. Oxford University Press, Oxford.

Pen, I., Weissing, F.J., 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. Proc. R. Soc. Lond. B 267, 2411–2418.

Queller, D.C., 1992. Quantitative genetics, inclusive fitness, and group selection. Am. Nat. 139, 540–558.

Queller, D.C., 2006. To work or not to work. Nature 444, 32–42.

Rankin, D.J., López-Sepulcre, A., Foster, K.R., Kokko, H., 2007. Species-level selection reduces selfishness through competitive exclusion. J. Evol. Biol. 20, 1459–1468.

Rankin, D.J., López-Sepulcre, A., 2005. Can adaptation lead to extinction? Oikos 111, 616–619.

Ridley, J., Yu, D.W., Sutherland, W.J., 2005. Why long-lived species are more likely to be social: the role of local dominance. Behav. Ecol. 16, 358–363.

Teyssèdre, A., Couvet, D., Nunney, L., 2006. Lower group productivity under kin-selected reproductive altruism. Evolution 60, 2023–2031.

Wenseleers, T., Helanterä, H., Hart, A., Ratnieks, F.L.W., 2004. Worker reproduction and policing in insect societies: an ESS analysis. J. Evol. Biol. 17, 1035–1047.

Wenseleers, T., Ratnieks, F.L.W., 2006. Enforced altruism in insect societies. Nature 444, 50.

West, S.A., Griffin, A.S., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–432.

Wilson, E., Hölldobler, O.B., 2005. Eusociality: origin and consequences. Proc. Natl. Acad. Sci. U.S.A. 102, 13367–13371.

Wong, B.B.M., Kokko, H., 2005. Is science as global as we think? Trends Ecol. Evol. 20, 475–476.