COMMENTARY
Cooperation within and among species

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Cooperation models are often idiosyncratic, and a recent objective has been to connect these models into a framework in which different forms of cooperation can be compared (Queller, 1985; Connor, 1995; Dugatkin, 1997; Frank, 2003; Sachs *et al.*, 2004). Lehmann & Keller (2006) (hereafter 'L&K') pursue this goal by building a synthetic mathematical framework of cooperation based on an expansion of Hamilton's inclusive fitness equation (Hamilton, 1964). L&K's model predicts specific conditions in which intra-specific cooperation can be maintained. Although, no equation can capture the complexity of nature, a fruitful outcome of this effort is to mathematically define and categorize the fundamental processes of cooperation.

I begin my comments by describing why cooperation is a significant problem and how it was initially approached by theoreticians. Subsequently, I remark on the challenges at hand when categorizing cooperative traits and behaviours using models. I make three main points: (i) One strength of L&K's framework is that it distinguishes benevolent behaviours that occur among relatives (altruism) vs. nonrelatives (cooperation). I re-examine this long-standing theoretical divide at the outset to counter a point that they highlight in their introduction. (ii) I review the conditions for cooperation that emerge from L&K's model and compare their findings to other approaches. I focus on their models for cooperation among nonrelatives such as by-product mutualism (West Eberhard, 1975; Brown, 1983; Connor, 1995; Sachs *et al.*, 2004) and reciprocity (Trivers, 1971; Axelrod & Hamilton, 1981; Bull & Rice, 1991; Sachs *et al.*, 2004) that parallel mutualism theory. By-products and reciprocity can explain both intra-specific cooperation and mutualism, and I suggest how predictions differ in these two arenas. (iii) L&K model intra-specific reciprocity with two components (repeated interactions and information) that are both required for the evolution of cooperation. Other frameworks have separated these components (Bull & Rice, 1991; Simms & Taylor, 2002; Sachs *et al.*, 2004). I compare these approaches and review empirical studies that show how information about potential partners can allow conspecifics to select cooperative individuals.

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The problem of cooperation

The evolution of cooperation is a central problem in biology. All targets of natural selection are thought to maximize their own fitness, and nonetheless, cooperative investment in others is ubiquitous. Cooperation can be found across taxa and it pervades all levels of biological organization from genes to cells to organisms to societies. However, selfish interests are a constant source of conflict that challenges the maintenance of cooperation. Any cooperative system can be thwarted by conflict, and many are. The results of such conflict range from selfish genes (Burt & Trivers, 2006) to cancerous cells (Michor *et al.*, 2003) to cheating symbionts (Sachs & Wilcox, 2006) to warfare (Boydon, 2004). How can cooperation evolve and be maintained in the face of conflict?

The study of cooperation has been split into complementary fields: the maintenance of cooperation within and among species. Hamilton's elegant theory of kin selection laid the groundwork for intra-specific cooperation (Hamilton, 1964). Hamilton proposed that the genes for cooperation tend to benefit copies of themselves in close relatives (Hamilton, 1964). Yet, nonrelatives commonly cooperate, so kin selection is only one explanation (Griffin & West, 2002). The theory of inter-specific cooperation (or mutualism) began with Trivers' model of reciprocal altruism (1971), in which cooperative benefits directed from one individual to another are returned to the first for a net fitness benefit. Shortly thereafter West-Eberhard described by-product mutualism (named by J. Brown), in which the benefits of a cooperative trait automatically outweigh any cost (West-Eberhard, 1975; Brown, 1983; Queller, 1985; Connor, 1995). Cooperation among nonrelatives represents a potential realm of overlap between mutualism and intra-specific theory. Trivers' original formulation of reciprocal altruism (1971) modelled intra-specific cooperation (among humans) as well as mutualisms (cleaning symbioses). Most theory that has stemmed from his work is focused solely on either intra-specific cooperation or mutualism, and rarely both.

Cooperation among relatives and nonrelatives

The most extreme forms of cooperation occur among relatives. An extraordinary aspect of kin-selected traits is that they can be detrimental or even deadly to the bearer (Hamilton, 1964). For instance, a bee that stings an invader to protect hive mates and loses her life in the process. This deadly behaviour cannot be favoured via direct reproductive benefits, but can be selected if the hive-mates share her genes. In contrast, cooperation with nonrelatives or other species can only be maintained when cooperative individuals survive to pass on their traits.

Cooperation with nonrelatives can be maintained because there is reciprocation (Trivers, 1971; Axelrod & Hamilton, 1981; Bull & Rice, 1991; Sachs *et al.*, 2004) or

because by-product benefits exist (West-Eberhard, 1975; Brown, 1983; Queller, 1985; Connor, 1995). Unlike kin selection, an explicit assumption of both types of models is that individuals gain direct fitness benefits from their cooperative traits (Queller, 1985; Sachs *et al.*, 2004). This is despite L&K's opening assertion that this distinction was not made or followed in a previous framework by Sachs *et al.* (2004). To clarify this further, Sachs and colleagues (2004) pointed out that: (i) the costs of cooperation are compensated by partners under reciprocation models (Sachs *et al.*, 2004, p. 139), (ii) by-product cooperation involves automatic benefits to the bearers of these traits (p. 145) and (iii) in contrast, under kin selected cooperation, individuals need not benefit directly from their benevolent acts (p. 143).

The conditions for cooperation

L&K delineate four conditions necessary for the evolution of cooperation. At least one of these conditions must be fulfilled for cooperation to be selected under their model. Two of the latter conditions (conditions three and four) presented in L&K's model fit squarely in the Hamiltonian framework of kin selection (1964). Condition three is the basic form of kin selected cooperation (Hamilton, 1964), 'preferential interactions with related individuals.' Condition four is a special case of this, 'genetic correlation between genes coding for altruism and phenotypes that can be identified' (Lehmann & Keller, 2006), known as greenbeard selection (Hamilton, 1964; Dawkins, 1976). Kin selection models (and their relationship with direct-benefit models) have been reviewed in depth elsewhere (Queller, 1985, 2000; Griffin & West, 2002; West *et al.*, 2002a) and I will not discuss them further.

L&K's first condition is a form of synergism (e.g. Queller, 1985)

The first condition that L&K discuss ('condition one') is the simplest form of cooperation. Condition one specifies 'direct benefits to the focal individual' (Lehmann & Keller, 2006) which L&K compare with by-product mutualism (Brown, 1983) and synergism (Queller, 1985). Their pleasingly simple accounting of condition one – in which the benefits of a cooperative trait outweigh the costs – can be further modified so that the cooperation is density or frequency dependent. The empirical cases suggest that direct benefits to intra-specific cooperation are always dependent on group size. The examples that L&K point out (group hunting, nest building and defence) provide advantage to cooperative individuals that varies with group size, and such behaviours are selected against if the group is too big or small. It is important to differentiate condition one from inter-specific by-product models, in which the cooperative trait exists irrespective of density. For instance, some species' physical by-products benefit individuals of another species (Brown, 1983), such as lions that provide

by-products to vultures in the form of prey remains. The lions likely abandon prey remains simply because their dentition does not allow them finish their kill, and such a trait is independent of groups size. L&K's condition one, in contrast, is analogous to intra-specific synergism – in which acts by two (or more) individuals benefit both more than if either had acted alone (Queller, 1985).

By-products cooperation in the literal sense, with beneficial transfer of useless physical by-products (or any unneeded resource), is likely rare among conspecifics because they have similar resource needs and produce similar by-products (Gauss, 1934). Mutual exchange of by-products among species may be common, and this exchange can promote the further evolution of cooperative traits (Connor, 1995; Sachs *et al.*, 2004). Schwartz & Hoeksema (1998) model the example in which two partners each can cheaply produce only one of two complementary resources, and trade of these resources promotes the evolution of cooperation. Their model focuses on inter-specific examples, likely because intra-specific cases of by-product exchange are rare. Although examples of complementary resources (and or needs) can be envisioned among conspecifics (i.e. interactions among sexes, ages, castes, or any type of class), the differences found within a species will rarely approach those among species. Cooperative traits that fulfil condition one, with direct benefits to the bearer, appear to be much more restrictive in scope within species than among them.

L&K's second condition is a form of reciprocity (e.g. Trivers, 1971)

L&K's second condition for cooperation is a form of reciprocity (Trivers, 1971). 'Condition two' occurs if there is 'information allowing a better than random guess about whether a given individual will behave cooperatively in repeated reciprocal interactions' (Lehmann & Keller, 2006). This mechanism is reminiscent of the famous iterated prisoner's dilemma (IPD) model of Axelrod & Hamilton (1981), which demonstrated that the choosy strategy of 'tit-for-tat' can maintain cooperation among nonrelatives when the likelihood of future interactions with the same partner is high. The tit-for-tat strategy is to cooperate when your partner has cooperated in the most recent iteration and refuse to cooperate if your partner did not cooperate in the most recent iteration. Whereas the IPD model offers an elegant solution to cooperation among nonrelatives, few empirical examples are thought to satisfy its assumptions (Noë, 1990; Noë & Hammerstein, 1994; Noë *et al.*, 2001; Bergstrom *et al.*, 2003; Sachs *et al.*, 2004).

Many researchers have found it useful to separate reciprocity into two components; repeated interactions of partners – partner fidelity – and the ability of interactants to alter their response based on the other's behaviour – partner choice or sanctions (Noë, 1990; Bull & Rice, 1991; Nowak & May, 1992; Noë & Hammerstein, 1994; Doebeli & Knowlton, 1998; Simms & Taylor, 2002; West *et al.*, 2002b; Sachs *et al.*, 2004). Many examples of

mutualism satisfy the assumptions of one of these separate mechanisms. Empirical work has shown that partner fidelity stabilizes inter-specific cooperation in a jellyfish-algal symbiosis (Sachs & Wilcox, 2006) while partner choice appears to stabilize legume-rhizobium symbioses (Kiers *et al.*, 2003; Simms *et al.*, 2006). L&K's model recognizes two components of reciprocity that are analogous to partner choice and partner fidelity. They model the probability of future interaction with a partner (w) and also model the probability of cooperating only with others that have cooperated in previous interactions (m), called 'information' or 'memory'. However, cooperation cannot evolve under L&K's model when $w = 0$ (no repeated interactions) and without some memory. The two components of reciprocity do not support cooperation independently under L&K's approach.

Can we conclude from L&K's model that partner fidelity and partner choice mechanisms cannot support intra-specific cooperation independently? There has long been controversy over the role of partner fidelity in cooperation, especially within species. Nowak & May (1992) modelled cooperative traits in viscous populations (which promote repeated interactions) and found that cooperation could be maintained without a choice mechanism. Other theoreticians have countered that local competitive interactions can override selection for cooperation in viscous populations (Taylor & Wilson, 1998; West *et al.*, 2002a; Lehmann & Keller, 2006), and this effect been shown empirically in bacteria (Griffin *et al.*, 2004). Separate from the debate over local competition, L&K assert that the mechanisms promoting cooperation in Nowak & May's model (1992) are actually kin selection. L&K's model shows that kin selection can favour cooperation in viscous populations as long as 'individuals are more related in altruistic than in competitive interactions' (Lehmann & Keller, 2006). A powerful aspect of L&K's approach is that it allows the dissection of the direct and indirect benefits of cooperation with spatial structuring, which is often difficult in intra-specific cooperation (West *et al.*, 2002a). By separating these forces, L&K's model posits that there are no conditions under which intra-specific cooperation can spread solely by partner fidelity, preferential interactions among kin is required.

We should consider predictions for inter-specific partner fidelity separately from L&K's model. There are two important distinctions between intra- and inter-specific partner fidelity. One difference is the intensity of competition: the theory of competitive exclusion suggests that inter-specific competition is less intense (Gauss, 1934), and therefore less likely to thwart partner fidelity systems among species (Sachs *et al.*, 2004). Further, inter-specific interactions are often characterized by exchange of complementary resources (Schwartz & Hoeksema, 1998), which can help initiate the evolution of partner fidelity (and choice) systems (Sachs *et al.*, 2004; Sachs & Bull, 2005). The second important difference is that vertical transmission offers a powerful mechanism to enforce partner fidelity among species

(Fine, 1975; Axelrod & Hamilton, 1981; Bull & Rice, 1991; Sachs *et al.*, 2004), and no analogous mechanism appears to exist within species.

Partner choice selects for intra-specific cooperation

Unlike partner fidelity, partner choice has long been considered sufficient for the maintenance of cooperation both within and among species (Noë, 1990; Bull & Rice, 1991; Noë & Hammerstein, 1994; Dugatkin & Sih, 1995; Noë *et al.*, 2001; Bshary & Noë, 2003; Sachs *et al.*, 2004). Here, I define partner choice as the ability of one individual to alter its response to others such that cooperative partners are offered disproportionate benefits. Partner choice selects for cooperation because cooperative partners are offered greater than average benefits, including the punishment of uncooperative partners (Sachs *et al.*, 2004). Models have predicted that partner choice mechanisms can act alone to support intra-specific cooperation (Eshel & Cavalli-Sforza, 1982; Noë, 1990; Noë & Hammerstein, 1994) and empirical examples appear to fulfil these predictions. Examples include nuptial gifts in scorpionflies (Thornhill, 1976, 1984) and bushcrickets (Gwynn, 1988), as well as coalitions in baboons (Noë, 1990) and common eiders (Ost *et al.*, 2003, 2005).

Mechanisms that are analogous to choice can be found in two parts of L&K's model. I have already discussed 'memory,' a component of condition two, which does not independently support cooperation. L&K also consider coercion, punishment and policing as facilitating mechanisms that can alter the cost-to-benefit ratio of cooperation, but these mechanisms require repeated interactions in their model (Lehmann & Keller, 2006). However, L&K do not consider partner choice in which cooperative partners are rewarded in the current interaction, and the empirical examples that I reviewed above all fit this description. Any future attempt to connect the field of cooperation under one framework should include the full spectrum of partner choice mechanisms.

Conclusions

L&K follow traditional paths in their categorization of cooperative traits. They stick to the Hamiltonian framework by separating cooperative traits that offer indirect benefits (among relatives) from those that can only offer direct benefits (among nonrelatives). Cooperative investment in nonrelatives is supported under their model because it is automatically beneficial (condition one) or because partners reciprocate benefits (condition two). Automatic benefits to cooperation are worthy of further study as they likely form the origin of more complex cooperative mechanisms. Yet, cooperation of this type appears restricted in scope within species, likely because conspecifics compete intensely and exhibit few complementary needs. Reciprocation of benefits is a common mechanism of cooperation and L&K's model of reciprocity follows from Axelrod Hamiltons's famous IPD game

(1981). The IPD game has dominated the field and its main flaw is also found in L&K's approach: partners are not allowed to choose among potential interactants but are forced into a dyadic repeated-interactions game. Partner choice, in which cooperative individuals are selectively offered benefits, is a main mechanism of cooperation that has been given short shrift because of the longstanding dominance of the IPD model (Noë, 1990; Bull & Rice, 1991; Noë & Hammerstein, 1994; Noë et al., 2001; Bshary & Noë, 2003; Sachs et al., 2004).

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References

Axelrod, R. & Hamilton, W.D. 1981. The Evolution of cooperation. *Science* **211**: 1390–1396.

Bergstrom, C.T., Bronstein, J.L., Bshary, B., Connor, R.C., Daly, M., Frank, S.A., Gintis, H., Keller, L., Leimar, O., Noë, R. & Queller, D.C. 2003. Interspecific mutualism. In: *Genetic and Cultural Evolution of Cooperation* (P. Hammerstein, ed.), pp. 241–256. MIT Press, Cambridge.

Boydon, S. 2004. *The Biology of Civilisation: Understanding Human Culture as a Force in Nature*. University of New South Wales Press, Sydney.

Brown, J.L. 1983. Cooperation-a biologist's dilemma. *Adv. Study Behav.* **13**: 1–37.

Bshary, R. & Noë, R. 2003. Biological markets: the ubiquitous influence of partner choice on the dynamics of cleaner fish-client fish interactions. In: *Genetic and Cultural Evolution of Cooperation* (P. Hammerstein, ed.), pp. 167–184. MIT Press, Cambridge.

Bull, J.J. & Rice, W.R. 1991. Distinguishing mechanisms for the evolution of co-operation. *J. Theo. Biol.* **149**: 63–74.

Burt, A. & Trivers, R. 2006. *Genes in Conflict: The Biology of Selfish Genetic Elements*. Harvard University Press, Cambridge.

Connor, R.C. 1995. The benefits of mutualism: a conceptual framework. *Biol. Rev.* **70**: 427–457.

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, New York.

Doebeli, M. & Knowlton, N. 1998. The evolution of interspecific mutualisms. *Proc. Nat. Acad. Sci. USA* **156**: 567–576.

Dugatkin, L.A. 1997. *Cooperation Among Animals: A Modern Perspective*. Oxford University Press, New York.

Dugatkin, L.A. & Sih, A. 1995. Behavioral ecology and the study of partner choice. *Ethology* **99**: 265–277.

Eshel, I. & Cavalli-Sforza, L.L. 1982. Assortment of encounters and evolution of cooperativeness. *Proc. Nat. Acad. Sci. USA* **79**: 1331–1335.

Fine, P.E.M. 1975. Vectors and vertical transmission: an epidemiological perspective. *Ann. NY Acad Sci.* **266**: 173–194.

Frank, S.A. 2003. Perspective: repression of competition and the evolution of cooperation. *Evolution* **57**: 693–705.

Gauss, C.F. 1934. *The Struggle for Existence*. Williams & Wilkins, Baltimore.

Griffin, A.S. & West, S.A. 2002. Kin selection: fact and fiction. *Trends Evol. Ecol.* **17**: 15–21.

Griffin, A.S., West, S.A. & Buckling, A. 2004. Cooperation and competition among pathogenic bacteria. *Nature* **430**: 1024–1027.

Gwynn, D.T. 1988. Courtship feeding in katydids benefits the mating male's offspring. *Behav. Ecol. Sociobiol.* **23**: 373–377.

Hamilton, W.D. 1964. The genetical evolution of social behavior, 1 & 2. *J. Theor. Biol.* **7**: 1–52.

Kiers, E.T., Rousseau, R.A., West, S.A., & Denison, R.F. 2003. Host sanctions and the legume-rhizobium mutualism. *Nature* **425**: 78–81.

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.

Michor, F., Frank, S.A., May, R.M., Iwasa, Y. & Nowak, M.A. 2003. Somatic selection for and against cancer. *J. Theor. Biol.* **225**: 377–382.

Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Anim. Behav.* **39**: 78–90.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**: 1–11.

Noë, R., Van Hooff, J.A.R.A.M. & Hammerstein, P. (eds). 2001. *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*. Cambridge University Press, Cambridge.

Nowak, M.A. & May, R.M. 1992. Evolutionary games and spatial chaos. *Nature* **369**: 826–829.

Ost, M., Vitikainen, E., Waldeck, P., Sundstrom, L., Hollmen, T., Franson, J.C. & Kilpi, M. 2005. Eider females form nonkin brood-rearing coalitions. *Mol. Ecol.* **14**: 3903–3908.

Ost, M., Ydenberg, R., Kilpi, R. & Lindstrom, K. 2003. Condition and coalition formation by brood-rearing common eider females. *Behav. Ecol.* **14**: 311–317.

Queller, D.C. 1985. Kinship, reciprocity and synergism in the evolution of social behavior. *Nature* **318**: 366–367.

Queller, D.C. 2000. Relatedness and the fraternal major transitions. *Philos. Trans. R. Soc. B.* **355**: 1647–1655.

Sachs, J.L. & Bull, J.J. 2005. Experimental evolution of conflict mediation between genomes. *Proc. Nat. Acad. Sci. USA.* **102**: 390–395.

Sachs, J.L., Mueller, U.G., Wilcox, T.P. & Bull, J.J. 2004. The evolution of cooperation. *Q. Rev. Biol.* **79**: 135–160.

Sachs, J.L. & Wilcox, T.P. 2006. A shift to parasitism in the jellyfish symbiont *Symbiodinium microadraticum*. *Proc. R. Soc. B.* **273**: 425–429.

Schwartz, M.W. & Hoeksema, J.D. 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology* **79**: 1029–1038.

Simms, E.L. & Taylor, D.L. 2002. Partner choice in nitrogen-fixing mutualisms of legumes and rhizobia. *Int. Comp. Biol.* **42**: 369–380.

Simms, E.L., Taylor, D.L., Povich, J., Shefferson, R.P., Sachs, J.L., Urbina, M. & Tausczik, Y. 2006. An empirical test of partner choice mechanisms in a wild legume-rhizobium interaction. *Proc. R. Soc. Lond. B.* **273**: 77–81.

Taylor, P.D. & Wilson, D.S. 1998. A mathematical model of altruism in haystacks. *Evolution* **42**: 193–196.

Thornhill, R. 1976. Sexual selection and nuptial feeding behavior in *Bittacus apicalus* (Insecta: Mecoptera). *Am. Nat.* **110**: 529–548.

Thornhill, R. 1984. Alternative female choice tactics in the scorpionfly *Hylobittacus apicalus* (Mecoptera) and their implications. *Am. Zool.* **24**: 367–383.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**: 35–57.

West, S.A., Kiers, E.T., Simms, E.L. & Denison, R.F. 2002a. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proc. R. Soc. Lond. B.* **269**: 685–694.

West, S.A., Pen, I. & Griffin, A.S. 2002b. Cooperation and competition between relatives. *Science* **296**: 72–75.

West-Eberhard, M.J. 1975. Evolution of social behavior by kin selection. *Q. Rev. Biol.* **50**: 1–33.