Cooperation Theory of Cooperative Breeding

Skubic, E.

IIASA Interim Report
December 2006

Interim Report **IR-06-059**

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December 2006

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Cooperative breeding is the joint raising of offspring by two or more individuals, where at least one of them is not the genetic parent of the young. The key characteristics of cooperative breeding systems are diversity of social behaviours within and between groups and high variation of factors influencing conflict over reproduction (for review see Komdeur, 2006). In the second half of the 20th century, development of research on cooperative breeding systems has been influenced by game theory from human economy (e.g. Nash, 1950; Maynard Smith, 1982; Hammerstein and Selten, 1994), by empirical studies on different systems (e.g. Brown, 1987; Taborsky, 1994; Solomon and French, 1997; Koenig and Dickinson, 2004), and by mathematical models of fitness advantages of group living in behavioural ecology (initiated mainly by Hamilton, 1964 and Vehrencamp, 1983). Cooperative breeding systems comprise a subset of social systems with cooperative behaviour, but are of high importance to generate hypotheses, search for patterns and mechanisms, and develop theories for the evolution of social life.

Mechanistic concepts to explain the evolution of cooperation (see e.g. Dugatkin, 1997; Hammerstein, 2003) have been developed parallel to the discoveries of the diversity of these behaviours. In this context, evolutionary theory uses mainly game theoretical arguments, where the strategy of one individual depends on the strategies of others in the population. Most approaches use non-cooperative game theory (for review see McNamara et al., 2006) where individuals compete with each other to maximize their fitness but where cooperation is not assumed in advance. To solve Darwin's puzzle of the evolution of cooperation by natural selection the Prisoner's dilemma game (formulated after the Flood-Dresher experiment, Flood, 1958), that involves rational players trying to maximize individual payoffs, was translated to biology. One reason why this scenario and its variants became very popular in behavioural ecology is that its basic from entails just a single, but easily comprehensible, cooperative interaction.

Bergmüller et al. (2007) point out that an integration of various approaches from different viewpoints is necessary for future research on cooperative behaviour. The authors show that local benefits such as group augmentation, tolerance (pay to stay) and social prestige may be related to more than one cooperation mechanisms. In my view, mainly five factors influence the research dynamics of theoretical and empirical studies on the way towards a cooperation theory of cooperative breeding.

Definitions

First, system complexity and manifoldness of behavioural phenomena may cause a diverse understanding and a variety of definitions used for apparently well known terms (cf. Lehmann and Keller, 2006 and commentaries; West et al., 2007). The definition of a behaviour should be operational. An individual may act or operate solitarily. Individuals may interact with others antagonistically (e.g. fight) or cooperatively. If an individual co-operates with another individual, they work together on one or more tasks (cf. also Brosnan and de Waal, 2002). For example, cooperative breeders raise offspring together, they share living space and various tasks. A cooperative act involves fitness costs and can therefore be viewed as investment. When individual A performs a cooperative act by e.g. making a resource available to individual B and B cooperates with A by performing the same or a different task the fitness consequences in terms of evolution remain unknown. Only knowing the total outcome of a cooperative act or of a series of acts enables classification as a certain cooperation mechanism, i.e. as an evolutionary mechanism that may favour cooperative behaviour. For example, if the result includes benefits for both individuals, reciprocity will be the respective mechanism; if individual A was assigned a cost and individual B was assigned a benefit, the behaviour of A can be viewed as altruistic, the behaviour of B as selfish and the corresponding mechanism would be exploitation or parasitism (see also Bergmüller et al., 2007). Cooperative behaviour of one individual cannot be viewed in isolation from the behaviour of others. Evolutionary persistence of cooperation requires that the resulting total fitness consequences include benefits at least for one of the participants.

State dependence

Second, evolutionarily stable strategies consist of sets of decision rules. The outcome of a single cooperative act may have immediate fitness consequences, but e.g. various stochastic or synergistic effects may reduce or increase its influence on lifetime fitness. In a series of interactions, cost/benefit relations as well as the availability of alternative options may change with time and, more importantly, with individual state. In state variable models of behaviour (for review see McNamara et al., 2001) current optimal decisions are determined in relation to future fitness expectations and single decision points may have an impact on the path of a trajectory. Specific cooperation mechanisms may be important at different times in a decision process and their combination may change with state and time. The common currency for comparing behavioural alternatives at each decision point is the expected total future number of surviving offspring under a specific action, i.e. the individual reproductive value. In time-delayed interactions the value of the return act cannot be directly compared to the value of the current act. To determine the effects of cooperative behaviour on fitness and decide about the evolutionary mechanism we have to take account of the different times when young are produced (McNamara et al., 2001; Skubic et al., 2004). Decision processes that depend on individual state and time provide realistic projections but complexity of cooperative breeding systems and methodology so far limited the number of studies using this state-variable approach in cooperative breeders.

A cooperative breeding association is often terminated by dispersal of subordinates to breed independently as analysed in a study of the population dynamics of cooperatively breeding dwarf mongooses (Lucas et al., 1997). This dynamic programming model determines equilibrium life history strategies based on age, status and relatedness as states, and with population structure and corresponding dispersal decision matrix emerging during the

calculation process. The model predicts the age structure in the population, and the proportion of subordinates. Future fitness expectations and mortality risk turned out to be very important for dispersal decisions of subordinates and variation in intra-group relatedness can generate variation in dispersal.

Individuals may cooperate in terms of one type of behaviour (e.g. staying together, helping) and operate antagonistically in terms of another (e.g. competing for reproductive opportunities) as in an analysis of sequential reproductive decisions of helpers (Skubic et al., 2004). This dynamic programming model shows the relative influence of life history and behavioural variables on the reproductive strategy in the cichlid 'Princess of Burundi'. The model predicts that the optimal strategy of a male helper should primarily depend on an increase in expulsion risk resulting from reproducing, on intra-group relatedness and on the capacity to sire offspring in a competitive situation with the breeder male. Proceeding from this model where breeder behaviour was assumed we have analysed state dependent cooperative breeding strategies of both helper and breeder in a dynamic game (Skubic et al., MS), where helpers decide about their reproductive strategy and breeders decide about the dynamics of their group. This approach allows to predict causes and consequences of cooperative breeding under a range of conditions, based on the fitness effects induced by each participant's actions.

Many important dynamic asymmetries in individual characteristics that can be easily covered by state dependent models, and asymmetries in the currencies exchanged in behavioural acts can be translated to the common currency of individual fitness (McNamara and Houston, 1986; McNamara et al., 2001). Theoreticians should be encouraged to investigate specific cooperative breeding systems, as well as less complex scenarios, involving different types of cooperation mechanisms by thinking in terms of state variable dynamics. Probably, the states considered will differ between taxonomic groups (e.g. size is mainly important in fish, while energy reserves are considered to be of major importance in birds), but the general principles will be the same. State dependence may involve several constraints but, given an individual is in a certain state at a given time, strategic behaviour will emerge from the decision process as a set of behavioural tactics. In terms of the theory of cooperation it is important that theoreticians as well as empiricists make clear in their studies, whether they aim at classifying the relevant mechanisms in a system, during the life histories of members of a population, or according to behaviour in a certain time window of cooperative associations between individuals.

Population dynamics

Third, behavioural interactions of cooperative breeders may create and influence different population structures. For example, in the 'Princess of Burundi' there is interdependence between individual distributions over body size, relatedness, sex roles and space (Dierkes et al., 2005). These structures are dynamic and may again influence behavioural interactions, i.e. there is population feedback in addition to social feedback (Skubic in prep.). For example, groups with small subordinates will more likely contain individuals that are highly related to each other and to one or both breeders. This, together with spatial grouping, will make cooperative behaviour towards kin more likely than towards individuals from other groups. However, we might also expect high within-group mortality or dispersal rate in a metapopulation with groups containing a large proportion of small subordinates. This might reflect high competition between adults and high extra-group mortality.

Population structure adds another level of complexity to the scheme of cooperation mechanisms proposed by Bergmüller et al. (2007). The theory of dynamic systems has mainly influenced models of population development in biology (see e.g. Maynard Smith, 1974; Hofbauer and Sigmund, 1998). Some studies focused on dispersal patterns in meta-populations to predict spatio-temporal variations (Ferrière and Michod, 1996; Ferrière and Le Galliard, 2001) and build a bridge from population dynamics to cooperative breeding (Pen and Weissing, 2000; Le Galliard et al., 2005). Population feedback on individual behaviour may be a mechanism that reduces conflict as shown in a recent model (Rankin, 2006). The study reveals that increasing density dependence (increasing strength of population feedback) is likely to limit the level of competition, reduce conflict and prevent the population from extinction. Game theoretical models including physiological population structure and adaptive dynamics (e.g. Metz and Diekmann, 1986) and non-linear feedback effects on population densities will be useful to investigate specific social behaviours. A combination of theoretical and empirical studies is needed to explain cooperation in specific populations. Discoveries in cooperative breeding systems already influenced a theoretical approach of economic decisions (see Weibull and Salomonsson, 2006). This model includes population dynamics and rational choice and shows that reproductive competition may be necessary to promote cooperation.

Dimension

Fourth, it is necessary to consider social behaviour as multi-dimensional (cf. Nonacs, 2000). An investment of individual A in individual B could be a response to changing conditions, behaviour of other individuals or changing population density. For example, when a female capuchin monkey increases the number of cooperative actions towards its offspring (e.g. protecting them through defence behaviours) when the alpha-male has been exchanged this does not mean that she cooperates more with or invests more in the offspring. Female care may be regarded to evolve according to reciprocity (the offspring will contribute to the mother's future fitness) or as by-product being merely a response to the increased mortality risk from attacks of the unrelated male. When predation risk is high fast growth resulting in quickly decreasing mortality risk is important for vulnerable young. When a female cichlid decreases resources provided for its offspring this does not mean a decrease in investment. A reduction resulting in lower egg mass may be a response to an increase in helper number (Taborsky et al., 2007), i.e. the female invests in having helpers that protect the young. The distribution of reproduction between same sex individuals may be controlled by the opposite sex (e.g. Magrath and Heinsohn, 2000). For example female control may be important to determine male reproductive skew (Cant and Reeve, 2002; Hamilton and Heg, 2007).

Complexity

Fifth, the current classification scheme proposed by Bergmüller et al. (2007) has to be extended. Direct reciprocity between the same individuals (e.g. individual A cooperates with B because B has cooperated with A, Trivers, 1971; Axelrod and Hamilton, 1981) may include group augmentation (Kokko et al., 2001) when helpers have a positive effect on young survival and breeders related to them produce more young in exchange (cf. Skubic et al., MS). Cooperation may result from indirect reciprocity (Alexander, 1987; Nowak and Sigmund, 1998a, 1998b) if individuals prefer to cooperate with those that have cooperated with others in the past (e.g. individual A cooperates with B because A has observed B cooperating with C).

Recent experiments demonstrated indirect reciprocity within species in humans (Wedekind and Milinski, 2000), and Norway rats (Spahni, 2005), and between species in cleaner fish and their clients (Bshary and Grutter, 2006; see also Bshary, 2002). The classification scheme proposed by Bergmüller et al. (2007) has not included generalized reciprocity (Rutte, 2004; Pfeiffer et al., 2005; Hamilton and Taborsky, 2005), where individuals prefer to cooperate with others based on anonymous social experience. In the simplest case individual A cooperates with individual B if e.g. individual C had cooperated with A in the past. This mechanism does not require specific knowledge about identity or behaviour of cooperation partners but may function via changes of hormonal state due to socially influenced experiences. The strategy is Markovian since only the outcome of the last encounter (private information) is important for the current behavioural decision. The propensity to cooperate is increased after positive experience delivered by a helpful act, not by experience of other positive effects of the environment (Schmid, 2005). If individual A cooperates with B because A has observed C cooperating with D, cooperation evolves via indirect generalized reciprocity. These mechanisms of reciprocal cooperation may complement each other or co-occur in the same system.

Bergmüller et al. (2007) show that concepts formulated in view of cooperative breeding systems may be connected to several cooperation mechanisms. They point out that payment can be viewed as reciprocity or pseudo-reciprocity. For example, subordinate cichlids may use their helping behaviour as "pre-emptive appeasement" to reduce aggression towards them (Bergmüller and Taborsky, 2005) and pay to stay and not be expelled from the group (Balshine-Earn et al., 1998). A reproductive skew model (Kokko et al., 2002) revealed that payment to stay in groups of unrelated individuals may require tight or moderate ecological constraints. When constraints are moderate a dominant may require a payment from an unrelated subordinate at the slightest fitness costs of the association to the dominant, whereas a related subordinate may voluntarily contribute if otherwise its presence would be very costly to a dominant. When the dominant would prefer the subordinate to stay it may give staying incentives of reproductive concessions or groups fail to form, but then the model predicts no payment to stay. Payment to reproduce (Roughgarden, 2004) has been regarded as a form of trade of help and access to reproduction and can be viewed to influence why individuals stay in a group or help.

Group augmentation and social prestige may apply within and between generations, as well as with private and public information. An individual that helps to augment the group may cooperate with a breeder that tolerates helper reproduction or with the young produced or recruited that will be helpful in the future. Both can be viewed as reciprocity or pseudo-reciprocity, depending on the sign of the fitness effects. Groups may be able to expand in some systems but as larger group size may increase group attraction of predators (e.g. Balshine et al., 2001) and intra-group competition (e.g. for shelters, Taborsky, 1985) group augmentation may not be possible in some systems or at certain stages of group development. Group augmentation can be neither related to reciprocity nor to pseudo-reciprocity. In some cases it may remain difficult to distinguish whether cooperation enhancing (positive) or decreasing (negative) fitness effects of an individual on a partner will stabilize cooperation.

Social prestige (Zahavi, 1995; Zahavi and Zahavi, 1997) is viewed as a benefit in terms of respect gained when individuals stay in their familiar (natal) group and help. A high value of prestige does not imply a high social status but may determine the access to high social positions and reproductive opportunities in the future. Social prestige was intended to be an alternative mechanism to group (multi-level) selection, kin selection and reciprocal altruism

(Zahavi, 2003). However, if the individuals that accord respect to the signaller benefit themselves from the provided help, the behaviour may be interpreted as a form of reciprocity (help is reciprocated by respect of prestige).

Conclusion

The classification scheme presented by Bergmüller et al. (2007) is a first step on the way towards a cooperation theory of cooperative breeding. It is important that empirical studies measure both, social behaviours and immediate as well as future fitness consequences (preferably in long-term studies), and enlighten the development of cooperation mechanisms. Reproductive skew models (reviewed in Johnstone, 2000) considered mainly local benefits such as increased group output, kin advantages and resource inheritance after social queuing; physiological constraints such as differences in fighting ability; ecological constraints on future independent breeding; and the social dominance hierarchy to be important for subordinates' reproductive share. It is a theoretical and empirical challenge to search for patterns of cooperative behaviours and mechanisms, specifically for their combinations within and between systems. For example, kin selection might be important early in ontogeny in many cooperative breeders while mechanisms of reciprocity will emerge later, or specifically in systems where large or old helpers are found to stay (e.g. Brouwer et al., 2005; Bergmüller and Taborsky, 2005; Dierkes et al., 2005). It is important to ask how these systems differ in terms of their cooperation mechanisms from others where helpers are recruited from outside groups.

The current methodologies available to develop models or analyse empirical data for more than two individuals are often time consuming. Therefore, theoretical analyses often make the simplifying assumption that an individual is considered to have an average expectation about the behaviour of others. However, when an individual cannot measure the contribution of another member of the group, this may affect evolutionary stability of group formation (Kokko, 2003). Field and lab biologists often record behaviours of several individuals and then focus on comparing distributions of behaviour between subsets. Mathematical methods such as time series analysis (e.g. Haccou and Meelis, 1994) or social network analyses (e.g. Croft et al., 2005; D.B. McDonald, personal communication) may become more important for investigating cooperative breeder interactions. It is a challenge for theoreticians to "digest" the various characteristics of cooperative breeding systems and develop mathematical formulations of the paths and knots between the different cooperation mechanisms, indicated in the classification scheme. The tree of cooperation mechanisms proposed by Bergmüller et al. (2007) is not sequential in terms of life history or action time, and specific classifications may not be mutually exclusive; but it is an interesting approach to capture different influences on social behaviour. The main difficulty is faced in relaxing the complexity of the systems to make meaningful projections of their biology (cf. Dieckmann and Law, 2000). Empirical and theoretical studies as well as the theory of cooperation and the theory of cooperative breeding should coevolve.

Where specific factors of cooperative breeding may apply depends on how cooperation mechanisms and cooperative behaviour are defined, on the structure and dynamics of the used classification scheme, and on the time window of focus. It is the right time to initialize discussion and thinking about a new cooperation theory of social systems and cooperative breeding is one of its most promising and fascinating phenomena.

Acknowledgements

References

Alexander, R.D. 1987. The Biology of Moral Systems, 1st Edition, Aldine de Gruyter, New York, NY, 301 pp.

Axelrod, R., Hamilton, W.D. 1981. The evolution of cooperation. Science 211, 1390–1396.

Balshine-Earn, S., Neat, F.C., Reid, H., Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. Behav. Ecol. 9, 432–438.

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., Werner, N. 2001. Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). Behav. Ecol. Sociobiol. 50, 134–140.

Bergmüller, R., Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement. Anim. Behav. 69, 19–28.

Bergmüller, R., Johnstone, R.A., Russell, A.F., Bshary, R. 2007. Integrating cooperative breeding into theoretical concepts of cooperation. Behav. Process., in press.

Brosnan, S.F., de Waal, F.B.M. 2002. A proximate perspective on reciprocal altruism. Hum. Nat. 13, 129–152.

Brouwer, L., Heg, D., Taborsky, M. 2005. Experimental evidence for helper effects in a cooperatively breeding cichlid. Behav. Ecol. 16, 667–673.

Brown, J.L. 1987. Helping and Communal Breeding in Birds. Ecology and Evolution, 1st Edition. Ser.: Monographs in Behavior and Ecology (Krebs, C., Clutton-Brock, T.H. (Editors)), Princeton University Press, Princeton, NJ, 354 pp.

Bshary, R. 2002. Biting cleaner fish use altruism to deceive image-scoring client reef fish. Proc. R. Soc. B 269, 2087–2093.

Bshary, R., Grutter, A.S. 2006. Image scoring and cooperation in a cleaner fish mutualism. Nature 441, 975–978.

Cant, M.A., Reeve, H.K. 2002. Female control of the distribution of paternity in cooperative breeders. Am. Nat. 160, 602–611.

Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D., Krause, J. 2005. Assortative interactions and social networks in fish. Oecologia 143, 211–219.

Dieckmann, U., Law, R. 2000. Relaxation projections and the method of moments. In: Dieckmann, U., Law, R., Metz, J.A.J. (Editors.), The Geometry of Ecological Interactions: Simplifying Spatial Complexity, 1st Edition. Ser.: Cambridge Studies in Adaptive Dynamics. Cambridge University Press, Cambridge, pp. 412–455.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E., Achmann, R. 2005. Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. Ecol. Lett. 8, 968–975.

Dugatkin, L.A. 1997. Cooperation Among Animals. An Evolutionary Perspective, 1st Edition, Oxford University Press, Oxford, New York, NY, 221 pp.

Ferrière, R., Michod, R.E. 1996. The evolution of cooperation in spatially heterogeneous populations. Am. Nat. 147, 692–717.

Ferrière, R., Le Galliard, J.-F. 2001. Invasion fitness and adaptive dynamics in spatial population models. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Editors.), Dispersal. Part I: Measures of dispersal: genetic and demographic approaches, 1st Edition. Oxford University Press, New York, NY, pp. 57–79.

Flood, M.M. 1958. Some Experimental Games. Mgmt. Sci. 5, 5–26.

Haccou, P., Meelis, E. 1994. Statistical Analysis of Behavioural Data. An Approach Based on Time-Structured Models, 1st Paperback Edition, Oxford University Press, Oxford, 396 pp.

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

Hamilton, I.M., Heg, D. 2007. Clutch size adjustments and skew models: effects on reproductive partitioning and group stability. Behav. Ecol., in press.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52.

Hammerstein, P. 2003. Genetic and Cultural Evolution of Cooperation, 1st Edition, MIT Press, Cambridge, MA, London

Hammerstein, P., Selten, R. 1994. Game theory and evolutionary biology. In: Aumann, R.J., Hart, S. (Editors.), Handbook of Game Theory With Economic Applications. Vol. II, 1st Edition. Elsevier Science, Amsterdam, pp. 929–993.

Hofbauer, J., Sigmund, K. 1998. Evolutionary Games and Population Dynamics, 1st Edition, Cambridge University Press, Cambridge, 323 pp.

Johnstone, R.A. 2000. Models of reproductive skew: a review and synthesis. Ethology 106, 5–26.

Koenig, W.D., Dickinson, J.L. 2004. Ecology and Evolution of Cooperative Breeding in Birds, 1st Edition, Cambridge University Press, Cambridge, 293 pp.

Kokko, H. 2003. Are reproductive skew models evolutionarily stable? Proc. R. Soc. B 270, 265–270.

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

Kokko, H., Johnstone, R.A., Wright, J. 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behav. Ecol. 13, 291–300.

Komdeur, J. 2006. Variation in individual investment strategies among social animals. Ethology 112, 729–747.

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 (with electronic enhancement).

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 (with electronic appendix; see also commentaries pp. 1377–1436).

Lucas, J.R., Creel, S.R., Waser, P.M. 1997. Dynamic optimization and cooperative breeding: an evaluation of future fitness effects. In: Solomon, N.G., French, J.A. (Editors.), Cooperative Breeding in Mammals, 1st Edition. Cambridge University Press, Cambridge, pp. 171–198.

Magrath, R.D., Heinsohn, R.G. 2000. Reproductive skew in birds: models, problems and prospects. J. Avian Biol. 31, 247–258.

Maynard Smith, J. 1974. Models in Ecology, 1st Edition, Cambridge University Press, Cambridge, 146 pp.

Maynard Smith, J. 1982. Evolution and the Theory of Games, 1st Edition, Cambridge University Press, Cambridge, 224 pp.

McNamara, J.M., Houston, A.I. 1986. The common currency for behavioral decisions. Am. Nat. 127, 358–378.

McNamara, J.M., Houston, A.I., Collins, J.E. 2001. Optimality models in behavioral biology. SIAM Rev. 43, 413–466.

McNamara, J.M., Binmore, K., Houston, A.I. 2006. Cooperation should not be assumed. Trends Ecol. Evol. 21, 476–478.

Metz, J.A.J., Diekmann, O. 1986. The Dynamics of Physiologically Structured Populations, 1st Edition. Ser.: Lecture Notes in Biomathematics, Vol. 68. Springer, Berlin, Heidelberg, New York, NY, 511 pp.

Nash, J. 1950. Non-cooperative games. Ph.D. Thesis, Princeton University, Princeton, NJ, 32 pp.

Nonacs, P. 2000. Measuring and using skew in the study of social behavior and evolution. Am. Nat. 156, 577–589.

Nowak, M.A., Sigmund, K. 1998a. The dynamics of indirect reciprocity. J. Theor. Biol. 194, 561–574.

Nowak, M.A., Sigmund, K. 1998b. Evolution of indirect reciprocity by image scoring. Nature 393, 573–577.

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. B 267, 2411–2418.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M., Bonhoeffer, S. 2005. Evolution of cooperation by generalized reciprocity. Proc. R. Soc. B 272, 1115–1120. (with electronic appendix).

Rankin, D.J. 2006. Resolving the tragedy of the commons: the feedback between intraspecific conflict and population density. J. evol. Biol., in press.

Roughgarden, J. 2004. Evolution's Rainbow. Diversity, Gender and Sexuality in Nature and People, 1st Edition, University of California Press, Berkley, CA, Los Angeles, CA, 474 pp.

Rutte, C. 2004. Influence of social experience on agonistic and cooperative behaviour. Ph.D. Thesis, University of Berne, Bern, 58 pp.

Schmid, R. 2005. Social and non-social influences on helpful behariour in Norway rats (*Rattus norvegicus*). M.Sc. Thesis, University of Berne, Bern, 48 pp.

Skubic, E., Hamilton, I.M., Taborsky, M. (MS). The dynamics of reproduction in cooperative breeders.

Skubic, E., Taborsky, M., McNamara, J.M., Houston, A.I. 2004. When to parasitize? A dynamic optimization model of reproductive strategies in a cooperative breeder. J. Theor. Biol. 227, 487–501.

Solomon, N.G., French, J.A. 1997. Cooperative Breeding in Mammals, 1st Edition, Cambridge University Press, Cambridge, 390 pp.

Spahni, C. 2005. Indirect reciprocity in Norway rats (*Rattus norvegicus*). M.Sc. Thesis, University of Berne, Bern, 58 pp.

Taborsky, B., Bruintjes, R., Skubic, E. 2007. Mothers adjust egg size to the amount of received help in a cooperatively breeding cichlid. Behav. Ecol., in press.

Taborsky, M. 1985. Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. Behaviour 95, 45–75.

Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. In: Slater, P.J.B., Rosenblatt, J.S., Snowdon, C.T., Milinski, M. (Editors.), Advances in the Study of Behavior, Vol. 23. Academic Press, San Diego, CA, pp. 1–100.

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

Vehrencamp, S.L. 1983. A model for the evolution of despotic versus egalitarian societies. Anim. Behav. 31, 667–682.

Wedekind, C., Milinski, M. 2000. Cooperation through image scoring in humans. Science 288, 850–852.

Weibull, J.W., Salomonsson, M. 2006. Natural selection and social preferences. J. Theor. Biol. 239, 79–92.

West, S.A., Griffin, A.S., Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. evol. Biol., in press.

Zahavi, A. 1995. Altruism as a handicap – the limitations of kin selection and reciprocity. J. Avian Biol. 26, 1–3.

Zahavi, A. 2003. Indirect selection and individual selection in sociobiology: my personal views on theories of social behaviour. Anim. Behav. 65, 859–863.

Zahavi, A., Zahavi, A. 1997. The Handicap Principle. A Missing Piece of Darwin's Puzzle, Oxford University Press, Oxford, New York, NY, 286 pp.