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PROJECT

Evolution of Cooperation Within and Between Species

Die Evolution des Lebens ist gekennzeichnet durch die sogenannten "großen evolutionären Übergänge", bei denen sich biologisch unabhängige Einheiten kooperativ zu komplexeren Systemen zusammenschlossen (unabhängige Replikatoren -> Chromosomen; Prokaryoten -> Eukaryoten; Einzeller -> Vielzeller). Diese komplexeren Systeme stellten revolutionäre Neuheiten dar und bilden heute neue Ebenen der Selektion. Ihre Entstehung wirft allerdings evolutionstheoretische Probleme auf: Wie und warum konnten sich egoistische, unabhängige Einheiten kooperativ zusammenschließen und erfolgreich fortbestehen?

In meinen Arbeiten dienen soziale Termiten als vergleichbare, aber leichter zugängliche Modellsysteme, um die Evolution kooperativer Assoziationen zu studieren. Hierbei kann ich das Auftreten von Kooperation auf zwei Ebenen experimentell untersuchen und analysieren: (i) Kooperation zwischen Individuen einer Art (Auftreten von "altruistischen" Arbeitern und Soldaten) und (ii) Kooperation zwischen zwei Arten (Symbiose zwischen Pilzzüchtenden Termiten und ihren Pilzen).

Während des Aufenthalts am Wissenschaftskolleg möchte ich u. a. theoretische Modelle zur Evolution von Kooperation auf beiden Ebenen entwickeln (Zusammenarbeit mit der Schwerpunktgruppe "Konfliktlösung in biologischen Systemen" um Francis Ratnieks) und als Mitherausgeberin an einem neuen Buch zur "Ökologie des Sozialverhaltens" arbeiten.

Lektüreempfehlung

Korb, J. and D. K. Aanen. "The Evolution of Uniparental Transmission of Fungus-Growing Termites (Macrotermitinae)." *Behavioral Ecology and Sociobiology* 53 (2003): 65-71.

Korb, J. and J. Heinze. "Multilevel Selection and Social Evolution of Insect Societies." *Naturwissenschaften* 91 (2004): 291-304.

Korb, J. and S. Schmidinger. "Help or Reproduce? The Influence of Food Availability on Kin-Based Altruism in the Drywood Termite *Cryptotermes secundus*."

Behavioral Ecology and Sociobiology 56 (2004): 89-95.

Evolution of Cooperation in Biological Systems

Cooperation plays a central role in the evolution of life. It is the common theme that characterises all major evolutionary transitions in which independent biological entities formed stages of higher complexity that constitute new levels of selection (independent replicators -> chromosomes; prokaryotes -> eukaryotes; individual cells -> multicellular organisms; individuals -> animal societies; Maynard Smith & Szathmáry 1995). However, such cooperation does not come about easily. Competition for limiting resources exists and natural selection generally favours selfish individuals that exploit them most successfully. How then can cooperation be stable given that cheaters (i.e. individuals with lower cooperative tendencies that avoid the costs of the cooperation and exploit cooperation) or freeloaders (i.e. cheaters that additionally prefer to group with cooperative individuals) are evolutionary favoured which lead to the break down of cooperation (freeloaders paradox; tragedy of the commons)? There are few problems if cooperation is 'for free' (mutualism), but generally there are costs involved and hence those individuals that cooperate are altruists.

Social insects (ants, bees, wasps, and termites) provide good model systems to study the evolution of cooperation. In contrast to the other levels of selection (see above) social insects are relatively easy to access and to manipulate. In such insect societies, individuals (workers, soldiers) forego own reproduction, even becoming sterile, to help other individuals reproduce. Generally, these altruists are helping close relatives to increase the reproductive success of close kin. Such a kin biased behaviour reflects one mechanism how costly cooperative behaviours can evolve: namely kin selection. Similarly, multicellular organisms are composed of closely related cells that share a common ancestry.

However, kin selection is only a special case of a general mechanism how cooperation can evolve: multi-level selection (trait group selection). Mathematical models that if there are structured populations in which altruists are more likely to associate among themselves than with cheaters (positive assortment) than cooperation can be selected. Although altruists may 'do worse' than selfish individuals within a group (negative within-group-selection), cooperation can be selected because groups with more altruists may 'perform better' than groups with few altruists (positive between-group-selection). Positive assortment within populations need not be based on direct recognition, but can be caused by many indirect mechanisms: e.g. kinship, non-uniform resource distribution, coevolution of group joining and cooperative behaviours, multigenerational groups, or reputation. In such structured populations between-group-selection also promotes the evolution of mechanisms that resolve and reduce conflicts within the groups as conflicts reduce group productivity. So policing of selfish individuals can arise which occurs similarly in insect societies, in multicellular organisms and at the genome level. The germ soma separation in multicellular organisms is seen as a mechanism to reduce the potential for conflict by limiting reproduction to a few cells and thus aligning the 'common interest' of the group. This separation parallels the evolution of worker sterility in large insect societies.

Social insects have for a long time been considered mainly in the framework of kin selection theory with a high emphasis on relatedness as the driving factor for social evolution. Recent results show however, that the kin component might have been overestimated: There are wasp societies that consist of unrelated individuals; in a group of basal termites kinship and helping relatives do not seem to be the driving force for individuals to become workers; colony organisation in many species is remarkable stable against variation in relatedness. Together all this suggests that between-group-selection (i.e. colony) may play an important role in insect societies. This underestimated aspect I want to investigate by applying multi-level selection approaches to social insects, especially termites.

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Inclusive fitness theory and eusociality

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