

Reproductive Strategies In Cooperative Breeders

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Goal

To develop a dynamic model that predicts the evolution of reproductive skew in cooperative breeders.

Background and motivation

Social systems are characterized by complex interactions between individuals, involving both cooperative behavior and reproductive competition between group members. Evolutionary mechanisms such as kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971; Nowak & Sigmund 1998), ecological constraints (Emlen 1982), prestige (Zahavi & Zahavi 1997), and similarity (Riolo et al. 2001) have been proposed to explain why social animals stay together and cooperate with each other.

Since the work of Vehrencamp (1979, 1983) the evolution of cooperative breeders has been studied in the framework of reproductive skew theory (see Johnstone 2000 and Reeve 2001 for reviews). Reproductive skew is defined as any unevenness in the partitioning of reproduction across members of a group. In particular, this approach aims at predicting the distribution of reproduction between dominant and subordinate group members (the latter are also called 'helpers'). The models assume that the possibility to increase own reproductive success may be an incentive to cooperate and live in groups, and predict the reproductive skew in a group as a function of factors such as relatedness, ecological constraints, group productivity, and depending on who controls reproduction. There also have been some attempts to explain delayed dispersal by dynamic models and to determine the importance of future fitness effects (Lucas et al. 1997; Kokko & Johnstone 1999; Ragsdale 1999; Kokko et al. 2002).

I argue that models formulated to explain the reproductive distribution in cooperative breeders have to incorporate further aspects of an animal's life history, such as (i) trade-offs between direct and indirect reproductive benefits, (ii) trade-offs between current and future benefits, (iii) repeated decision options, (iv) the dynamics of the conflict of interest between dominants and subordinates, and (v) realistic measures of the different fitness costs and benefits associated with the behavioral alternatives. I used a state space approach (see Houston & McNamara 1999 for an introduction to dynamic state variable models) to cover these different aspects of behavioral strategies of helpers (Skubic et al. ms) of the social cichlid fish *Neolamprologus pulcher* to predict optimal reproductive decisions. This approach revealed that behavioral strategies of subordinates (determining whether to refrain from reproducing or to parasitize the reproduction of dominant breeders) depend on a complex interplay between reproductive benefits and life-history costs. The risk of expulsion when helpers parasitize the breeders' reproduction turned out

to be of major importance for the reproduction of subordinates. In particular, I have shown that there are two thresholds, with parasitism optimal for small fish and large fish, but not optimal at intermediate size. Thus, a conditional reproductive strategy might be expected in subordinates: (i) while small, these would start to reproduce shortly after maturity (as found in many fish species; Taborsky 1994), and (ii) once large, helpers would invest into long-term survival, and future reproduction in an own territory.

In general, social animals have to pass through a phase of subordinate status during their life history before being able to become breeders and maintain a territory of their own. Depending on their growth rate, some individuals might reach a critical body size at which to become independent from their natal group more quickly than others. This suggests that reproductive strategies might be polymorphic during life history. Especially in fish, but also in mammals and social insects, fighting ability and female fecundity increase with body size. The body size of an individual relative to its competitors and thus the distribution of body sizes within a population may strongly influence the opportunity of a given individual to reproduce independently. The size distribution and the frequency of different reproductive strategies may therefore be important aspects of social systems and a model that links individual behavior to population dynamics is needed. To incorporate such population-level feedback into models of reproductive skew, by using methods from the theory of adaptive dynamics, is thus the primary goal of my summer project.

Research questions

I will determine evolutionary outcomes of behavioral evolution affecting reproductive skew in populations of cooperative breeders. The specific topics I plan to study during my research stay at IIASA are the following:

- To determine the evolutionarily stable body sizes for switching from one reproductive strategy to another.
- In this context, to investigate the evolutionarily stable coexistence of alloparental brood care, reproductive parasitism, and breeding in an own territory.
- To compare the effect of different ecological environments on the distribution of reproduction within social systems.

Methods and work plan

I will consider the social cichlid *N. pulcher* as a model system and extend my previous approach of dynamic programming by developing a population model that links individual decisions affecting reproduction to population dynamics. I assume that all individuals invest in alloparental brood care and defense, i.e., that they help in raising offspring, potentially of other group members. At any point in their life, individuals can 'decide' whether they (i) do not reproduce on their own, (ii) parasitize the reproduction of dominants, or (iii) try to obtain a territory of their own and become a dominant breeder. The corresponding shifts in reproductive strategy are assumed to be irreversible.

I will develop a deterministic size-structured population model assuming that individuals invest in care for non-descendant kin when they are small and switch to reproduction at larger body sizes. Body size and growth are continuous life-history variables, and we consider a continuum of possible switch sizes from pure helping to

parasitic reproduction and to breeding. Thus, the switch sizes from one reproductive role to another are the phenotypic variables of interest. First, I will assume two switch size variables in the model.

The population is characterized by the densities of the different reproductive roles. I incorporate an environmental feedback by taking the dynamics of density-dependent individual growth into account. The frequency distributions of the reproductive roles are considered to be strongly determined by size-dependent predation, the expulsion probability of helpers, and by the help that other individuals provide. I assume that the density of helping individuals results in fitness benefits in terms of fertility and growth (the helper effect). Population densities vary according to processes of size-dependent growth, fertility, and mortality. Spatial structure is included implicitly.

For numerical analysis, I will use the approximation of envisaging a continuously size-structured population as a collection of many size cohorts, characterized by their average body size and by the number of individuals they contain. This method is known as the 'Escalator Boxcar Train' (Tuljapurkar & Caswell 1997). I will determine the population dynamics of the resident strategy and determine the equilibrium size distributions of the three reproductive roles.

To analyze the evolutionary change of switch sizes I will apply methods of adaptive dynamics theory. Following other game theoretic approaches I assume that mutations occur rarely and that successful invasion by a mutant implies its replacing the resident strategy. Each resident set of switch sizes will result in stable equilibrium size distributions of non-reproducing, parasitizing, and breeding individuals. I then will consider mutant strategies that slightly deviate from the resident population strategy in their switch sizes and determine their invasion fitness. On this basis I will determine the selection gradient and thus the evolutionary attractor in the trait space of switch sizes.

The following scenarios will be investigated:

- To start I will examine the fitness consequences of the model described above with two possible switch size variables. In this analysis I assume that there are no differences in the reproductive roles between the sexes. However, there may be a variation in the equilibrium switch sizes between them and equilibrium solutions of both types will be examined separately.
- In a second approach I will allow for a difference in the roles between females and males and include the possibility of a non-reproductive phase before becoming a breeder.
- Thirdly, I will examine the influence of different environmental effects on the equilibrium densities of helpers, reproductive parasites, and breeders. In particular, the evolutionarily stable reproductive strategies will be investigated in response to a variation in mortality due to predation and in the helper effect.

I will use the deterministic model to determine possible evolutionarily singular points and examine their properties based on pairwise invasibility plots. Lastly, if time permits, I will construct a stochastic individual-based version of the model to investigate the robustness of the derived predictions.

Relevance and link to ADN's research plan

Including the environmental feedback between individual reproduction and population regulation, this adaptive dynamics study will determine evolutionary pathways of reproductive strategies involving cooperative breeding behavior. Understanding the effect of different environmental settings on these strategies will allow to compare data from different populations and species, and might propose a general pattern for explaining the observed high natural variation in cooperative behavior and reproductive skew.

Based on a model by Claessen & Dieckmann (2002), continuous-time adaptive dynamics (Dieckmann 1997; Tuljapurkar & Caswell 1997; Dieckmann 2003) will be used. The proposed project is related to ADN's research foci on the foundations of adaptive dynamics, on the evolution of cooperation, and on fisheries management. In particular, I will extend the application of adaptive dynamics models to understanding reproductive skew in the evolution of social systems.

Expected output and publications

The research described here might be integrated in one chapter of my PhD thesis and is expected to be published in a jointly authored paper in an international scientific journal.

References

- Claessen, D. & Dieckmann, U. (2002). Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Evolutionary Ecology Research*, 4:189-217.
- Dieckmann, U. (1997). Can adaptive dynamics invade? *Trends in Ecology and Evolution*, 12:128-131.
- Dieckmann, O. (2003). A beginners guide to adaptive dynamics. Univ. Utrecht.
- Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *The American Naturalist*, 119: 29-39.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology*, 7:1-52.
- Houston, A. I. & McNamara, J. M. (1999). *Models of adaptive behaviour. An approach based on state*. 1st edn. Cambridge: Cambridge Univ. Press.
- Johnstone, R. A. (2000). Models of reproductive skew: a review and synthesis. *Ethology*, 1:5-26.
- Kokko, H. & Johnstone, R. A. (1999). Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London B*, 266:571-578.
- 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? *Behavioral Ecology*, 13:291-300.

- Lucas, J. R., Creel, S. R. & Waser, P. M. (1997). Dynamic optimization and cooperative breeding: an evaluation of future fitness effects. In: *Cooperative breeding in mammals* (Ed. by N. G. Solomon & J. A. French), pp. 171-198. Cambridge: Cambridge Univ. Press.
- Nowak, M. A. & Sigmund, K. (1998). The dynamics of indirect reciprocity. *Journal of Theoretical Biology*, 194:561-574.
- Ragsdale, J. E. (1999). Reproductive skew theory extended: the effect of resource inheritance on social organization. *Evolutionary Ecology Research*, 1:859-874.
- Reeve, H. K. & Keller, L. (2001). Tests of reproductive-skew models in social insects. *Annual Reviews of Entomology*, 46:347-385.
- Riolo, R. L., Cohen, M. D. & Axelrod, R. (2001). Evolution of cooperation without reciprocity. *Nature*, 414:441-443.
- Skubic, E., Taborsky, M., Houston, A. I. & McNamara, J. M. ms. When to parasitise? A dynamic optimization model of reproductive strategies in a cooperative breeder.
- Taborsky, M. (1994). Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. In: *Advances in the study of behavior* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon & M. Milinski), Vol. 23:pp. 1-100. San Diego: Academic Press.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46:35-57.
- Tuljapurkar, S. & Caswell, H. (1997). *Structured-population models in marine, terrestrial, and freshwater systems*. 1st edn. New York: Chapman & Hall.
- Vehrencamp, S. L. (1979). The roles of individual, kin, and group selection in the evolution of sociality. In: *Social behaviour and communication* (Ed. by P. Marler & J. G. Vandenbergh), pp. 351-394. New York: Plenum Press.
- Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, 31:667-682.
- Zahavi, A. & Zahavi, A. (1997). *The handicap principle. A missing piece of Darwin's puzzle*. edn. Oxford, New York: Oxford Univ. Press.