# Mom made me do it: Division of labor via maternal effects

Mauricio González-Forero

*University of Tennessee, Knoxville, TN, USA*

*mgonzal7@utk.edu*

Mareen E. Hofmann

*Potsdam Institute for Climate Impact Research, Potsdam, Germany*

*Freie Universität Berlin, Germany*

*mareen.hofmann@pik-potsdam.de*

Sunday 23rd August, 2009

**Abstract**

Major transitions in evolution are mediated by the evolution of division of labor and elaborated communication. The evolution of division of labor is commonly explained as a consequence of the evolution of cooperation. Another possibility is that division of labor is a consequence of manipulation. The distinction is not merely semantic as the genes for helping are not located in the helper individual, but in the manipulating individual, introducing indirect genetic effects dynamics. We build an individual-based model to explore the conditions in which a manipulator can invade a population of non-manipulators. We consider the possibility of resistance to manipulation and study its evolution. Interestingly, the model illustrates the match between low resistance to manipulation and high reproductive capacity, which is consistent with evidence from Hymenoptera.

## Introduction

Major transitions in evolutionary history have involved the origin of upper levels of organization: for example, replicating molecules grouped into primordial

cells, eukaryotic cells grouped into multicellular organisms, and multicellular organisms grouped into eusocial colonies (Buss, 1987, Maynard Smith and Szathmáry, 1995). In a transition in levels of organization, entities that are capable of independent replication before the transition are only part of a larger replicating whole after it. Proposed yardsticks for such a transition include division of reproductive labor and elaborated communication among parts: after division of reproductive labor is established, members of the group are refrained from independent replication as they are ill-equipped to live in isolation; in addition, elaborated communication increases group cohesion and redistribution of benefits and costs, which prevents individuals from acting selfishly (Frank, 2003; e.g., quorum sensing in bacterial biofilms, gene organization into chromosomes, and chemical communication in insects). However, the evolution of division labor remains a challenge to evolutionary theory.

One of the best studied cases of division of reproductive labor is given by Hymenoptera (ants, bees and wasps). All species of ants and some of bees and wasps show division of reproductive labor, and hence possess colonies with reproductive and non-reproductive castes. Complete division of reproductive labor in insects is termed eusociality, and eusocial colonies are considered to constitute upper level individuals (Hölldobler and Wilson, 2009). In eusocial colonies, non-reproductives invest their efforts on housekeeping tasks, such as helping reproductives raise their brood, and typically do not reproduce themselves. The question of how Hymenopteran eusociality evolved has not been settled. It is currently agreed that the scenario must have been as follows: the Hymenopteran ancestor exhibited subsociality (i.e., maternal care of offspring); a subsequent stage was the evolution of sibsociality (i.e., offspring provide care to new, sister broods); finally, from sibsociality, eusociality evolved, where siblings providing care permanently relinquish their own reproduction. However, each step involves a decreasing investment in reproduction that is not obviously explained by evolutionary theory.

One possibility is that non-reproductive castes constitute cooperators, where genes for helping are located in the helper individual (Frank, 1998). Under kin selection, cooperation can spread in a population only if Hamilton's rule holds (Hamilton, 1964): $r > c/b$, where $r$ is the genetic relatedness between the cooperator and the recipient, $b$ is the increase in number of recipient's offspring after receiving help, and $c$ is the decrease in number of cooperator's offspring after providing help. Hence, high relatedness promotes the evolution of cooperation. Initially, it was considered that the fact that all Hymenopteran species are haplodiploid, where males are haploid and females are diploid, made Hymenoptera particularly prone to evolving cooperation. Haplodiploidy causes females to be more related to their sisters ($r = 3/4$) than to their offspring ($r = 1/2$). However, females are less related to their brothers ($r = 1/4$) than to their offspring and thus the average relatedness is equal towards siblings or offspring. This second fact poses a problem to the purportedly haplodiploid facilitation of the evolution of cooperation because helpers should have been capable of two things: identifying females, and helping them more often than males. It has been shown that this so-called greenbeard effect is unstable, so in this set-

ting haplodiploidy does not enhance the chances of cooperation (Lehmann and Keller, 2006). This and other reasons have limited the ability of haplodiploidy to explain the evolution of cooperation in Hymenoptera.

Another possibility is that non-reproductive castes are manipulated individuals who provide help in response to manipulation from social partners. In this view, the genes for helping are not located in the helper but in its social partners. Importantly, this introduces indirect genetic effects, and thus Hamilton's rule takes the form: $r + \rho_{dk} > c/b$, where $\rho_{dk}$ is the regression coefficient of direct effects of genes on their kin effects due to pleiotropy (Wolf *et al.*, 1998). Hence, if $\rho_{dk} > 0$, manipulation will have more potential to evolve than cooperation. However, it is argued that there is little evidence to support a manipulative origin for eusociality and that eusociality should be more common if it had originated by manipulation (Ratnieks and Wenseleers, 2008). Nonetheless, manipulation remains an unexplored avenue, and more directed theoretical studies can pinpoint potentially overlooked sources of evidence.

A verbal model for the evolution of Hymenopteran eusociality addresses the transition from subsociality to sibsociality by means of maternal manipulation (Linksvayer and Wade, 2005). It postulates that the genes for maternal care already present in an individual are induced by its mother to be expressed before the individual reaches reproductive age. Thus, the manipulated individual is expected to provide care to its siblings. The induction can be via zygotic genes or via behavioral mechanisms (e.g., poor feeding, thus inducing poor development in offspring, which are thus unable to reach reproductive age).

Here we explore the evolution of maternal manipulation by means of an individual-based model. We evaluate the conditions in which a mutant with the manipulation trait can invade a population of non-manipulators. We consider the possibility that individuals can resist manipulation. In addition, we study the evolution of resistance to manipulation.

# Model

## Overview

The purpose of the model is to understand the conditions under which one mutant manipulator can invade a population of non-manipulators and how different levels of resistance to manipulation might evolve. For this purpose, the model considers a *mutant* population of ants and a *wild* population of ants, each of which is associated with a certain *resistance probability*. The resistance probability is a crucial parameter that distinguishes the two populations under consideration. It refers to the probability that each single offspring can resist maternal manipulation and is able to be reproductive itself. Thus, the resistance probability is a value between 0 and 1. If the resistance probability of a population is 1, then there is no maternal manipulation, i.e., the population consists of all reproductive individuals. In this way, the model captures the special case of a population of non-manipulators. In the following, we refer to

reproductive individuals as *manipulators*, whereas non-reproductives are called *manipulated-ones*. The world these ant populations live in is a torus of $20 \times 20$ patches of grass, which serves as food for the ants.

## State variables and parameters

The model considers five different kinds of agents: manipulators of wild type, manipulated-ones of wild type, manipulators of mutant type, manipulated-ones of mutant type, as well as the patches on which the ants are located. We note that, as mentioned above, a population whose resistance probability is 1 consists of only reproductive individuals and there are thus no manipulated-ones in this population. Each ant is characterized by its

- *Energy*: Each ant needs a certain amount of energy for staying alive as well as for reproduction. Energy can be taken up by eating grass.

- *Age*: Each ant has a certain age, which increases by 1 for each time step. There is a maximum age the ants can attain.

Additional state variables of the manipulators are the *number of wild manipulated neighbors* and the *number of mutant manipulated neighbors*. The patches on the other hand are characterized by their amount of *grass*. Furthermore, the behavior of all of these agents depends on certain parameters. We refer to Table 1 for a complete list of these parameters, the type of agent each parameter is referring to, its definition, and default value.

## Process overview and scheduling

Within each time step, the following phases are processed for each ant in the following order (Figure 1 depicts a flow chart of these phases and their scheduling):

1. Metabolism: In this phase, the energy of each ant is reduced by the amount of energy specified by the parameter metabolism.

2. Mortality: In this phase, an ant dies if it has either attained the maximum age given by max-age, or if it does not have enough energy, i.e., if energy $<$ 0.

3. Dispersal: Here, every ant checks the grass available on its patch. If resources are depleted (i.e., grass $= 0$) and the ant is a manipulator, it moves $5 * $ stride-length in a random direction (dispersal). Otherwise, the ant moves a stride-length forward in a random direction (foraging).

4. Eating: If there is grass on the patch the ant is on, the ant consumes one unit of grass. This means that its energy increases by the amount of energy specified by the parameter grass-energy. At the same time, the amount of grass on this patch is decreased by 1.

| parameter | type of agent | definition | default value |
|---|---|---|---|
| max-age | all ants | maximum age each ant can attain | 10 |
| metabolism | all ants | amount of energy each ant consumes in one time step | 0.5 |
| stride-length | all ants | distance each ant moves in one time step if resources are sufficient; if the ant is a manipulator and there is no grass on the patch where the manipulator is situated, it can move $5 \times$ stride-length | 0.1 |
| resistance-probability | all ants | parameter distinguishing the two types of populations; it refers to the probability that one offspring of a manipulator can resist manipulation, i.e., that the offspring can reproduce itself instead of providing care for its siblings | varying values |
| kin-recognition | all ants | parameter that determines whether manipulated-ones can recognize their kin; if kin-recognition = 1, they are able to differentiate between the populations and help raising offspring only from their population; if kin-recognition = 0, they are not able to differentiate | 0 or 1 |
| reproductive-capacity | manipulators | maximum number of offspring an ant can have | 10 |
| reproduction-cost | manipulators | the amount of energy it takes for reproduction | 0.2 |
| grass-energy | patches | the amount of energy one unit of grass provides to an ant | 0.71 |
| max-grass-height | patches | determines the maximum number of grass units each patch can provide | 5 |

Table 1: List of parameters

5. Reproduction: If the ant is a manipulated-one, it does not reproduce and therefore goes immediately to the next phase. Furthermore, if the ma-

nipulator does not have enough energy for reproduction (i.e., energy $-$ reproduction-cost $< 0$), it is not reproducing as well and goes on to the next phase. Now, if a manipulator has sufficient energy for reproduction, its energy is lowered by the amount of energy specified by the reproduction-cost. All of its progeny is going to be of the same type as the manipulator (that is, either of wild or mutant type) and each offspring is going to be a manipulator with the resistance-probability specific of the type of population the parent manipulator belongs to. The number of progeny generated by the manipulator depends on the number of wild and mutant manipulated-ones in its neighborhood (i.e., all the manipulated-ones on the same patch as the manipulator and the manipulated-ones on the 8 directly surrounding patches) and whether there is kin recognition. More specifically, if a manipulator $M_i$ is of type $i$ for $i \in \{\text{wild}, \text{mutant}\}$, the number of its progeny $p(M_i)$ is given by

$$p(M_i) = 1 + \text{neighbors}_i + (1 - \text{kin-recognition}) * \text{neighbors}_j \qquad (1)$$

where $j \neq i$, $j \in \{\text{wild}, \text{mutant}\}$ refers to the type of population the considered manipulator does not belong to; $\text{neighbors}_i$ and $\text{neighbors}_j$ refer to the number of manipulated-ones in the neighborhood of the manipulator of type $i$ and $j$, respectively. Equation 1 is used as long as

$$\text{neighbors}_i + (1 - \text{kin-recognition}) * \text{neighbors}_j < \text{reproductive-capacity},$$

that is, until the reproductive capacity of the manipulator is attained. Otherwise, we set

$$p(M_i) = 1 + \text{reproductive-capacity}.$$

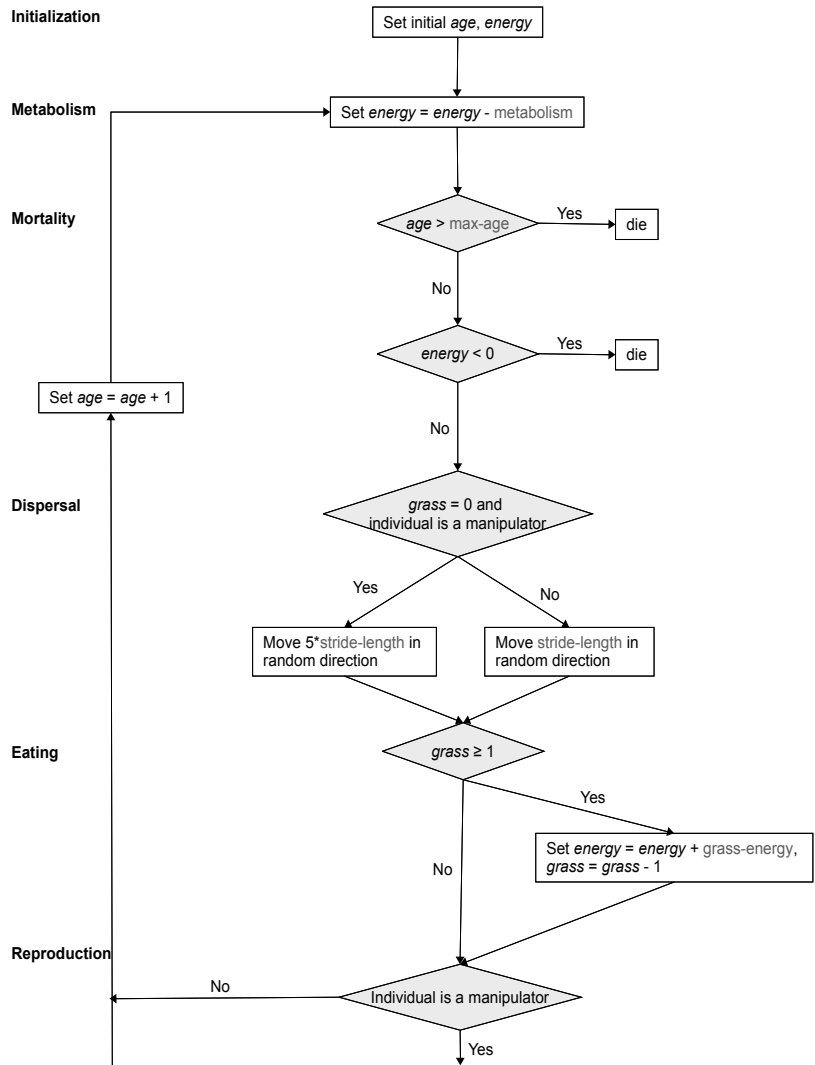6. Aging: The *age* of the ant is increased by 1.

As for the initialization, we start with altogether 100 ants of both populations: 99 manipulators of wild type and 1 mutant manipulator. Furthermore, the age of each of these ants is set at random to a number between 0 and max-age according to a discrete uniform distribution. The initial energy of each ant is set to the parameter metabolism.

In addition, there is the phase *grow-grass* being processed for each patch at the end of the time step, i.e., after the phases have been processed for each of the ants. It increases the amount of grass on the patch by 1 unit if the amount of grass on this patch is less than max-grass-height. Otherwise, the amount of grass is set to max-grass-height. Initially, the height of the grass in each patch is set to max-grass-height.

## Results

We identify several factors promoting the invasion of manipulators: kin recognition present, increasing stride length, increasing reproductive capacity, and
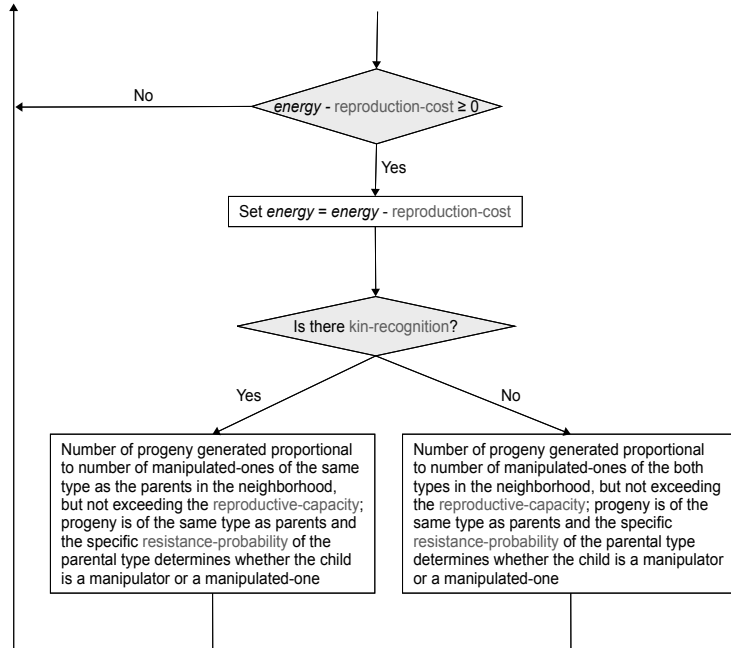
*For each individual:*

**Initialization**  →  Set initial *age, energy*

**Metabolism**  →  Set *energy* = *energy* - metabolism

**Mortality**  →  *age* > max-age — Yes → die
No

*energy* < 0 — Yes → die
No

Set *age* = *age* + 1

**Dispersal**  →  *grass* = 0 and individual is a manipulator

Yes → Move 5*stride-length in random direction

No → Move stride-length in random direction

**Eating**  →  *grass* ≥ 1 — Yes → Set *energy* = *energy* + grass-energy, *grass* = *grass* - 1
No

**Reproduction**  →  Individual is a manipulator — No
Yes

Figure 1: **Flow chart outlining the processes and the scheduling of the model.** Italicized words refer to state variables, whereas words in grey color represent parameters of the model.

increasing resistance to manipulation. The requirement of kin recognition is consistent with the idea that kin recognition occurred already in the Hymenopteran ancestor. Too small stride length prevented the invasion of manipulators due to the fact that manipulated offspring do not disperse, and since manipulators will only disperse too closely, manipulators are less likely to find patches with resources available. Furthermore, increasing reproductive capacity constituted the crucial advantage of manipulators over non-manipulators; this is because manipulators can leave more offspring due to the help they receive from manipulated individuals. However, the evolutionary stability of manipulation is not straightforward. Low resistance to manipulation causes manipulators to produce too few fertile offspring, thus manipulators with lowly resistant offspring were at a disadvantage. Thus, a mutant with decreasing resistance to manipulation typically did not invade a non-manipulator population. However, since resistance to manipulation is expected to be low in extant ant species, we evaluated the adaptive dynamics of resistance to manipulation more closely.

We evaluated whether low-resistance manipulators could invade high-resistance manipulators. Invasion did not proceed, for the parameter values checked, except when reproductive capacity was significantly increased. The increase in reproductive capacity was applied to both wild and mutant populations, and hence the only new mutation evaluated in this case was less resistance to manipulation. The reason for larger reproductive capacity to favor invasion of low-resistance mutants is that with a significantly large reproductive capacity, a manipulator producing a lower fraction of fertile offspring will still produce significant numbers of them. The matching between low resistance to manipulation and high reproductive capacity in principle aggrees with the pattern observed in increasingly advanced ant colonies.

## Discussion

The model evaluates the feasibility of the evolution of maternal manipulation giving rise to eusociality. It considers the relevance of resistance to manipulation, and identifies that resistance can decrease with increasing reproductive capacity. It suggests a scenario for the evolution of manipulation as follows: 1) A non-manipulating population is invaded by manipulating individuals with high resistance to manipulation, 2) a high-resistance population possesing high reproductive capacity is invaded by low-resistance manipulators. The intermediate step between 1) and 2) requires the evolution of larger reproductive capacity. One mechanism is given by improved fungal cultivation techniques among extant fungus-growing ants: species growing fungus on insect feces and corpses, or dead vegetable material form colonies in the low hundreds; those growing fungus adding fruit or flower parts have colonies in hundreds to low thousands; those using fresh leaves, stems, flowers and fruit have colonies of thousands to millions (Hölldobler and Wilson, 2009).

Manipulation provides an alternative for the evolution of division of labor without appealing to cooperation (the distinction being that the genes for help-

ing are not in the helper but in a social partner). This model of indirect genetic effects evaluates conditions for its evolution and points to the tradeoffs imposed by resistance to manipulation. Resistance to manipulation is a feature that needs further study in order to fully appreciate the feasibility of manipulation over cooperation for the evolution of division of labor.

# Acknowledgments

# References

Buss, L. W. (1987). *The Evolution of Individuality*. Princeton University Press, Princeton, NJ.

Frank, S. A. (1998). *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.

Frank, S. A. (2003). Repression of competition and the evolution of cooperation. *Evolution*, **57**, 693–705.

Hamilton, W. D. (1964). The genetical evolution of social behaviour I. *J. Theor. Biol.*, **7**, 1–16.

Hölldobler, B. and Wilson, E. O. (2009). *The Superorganism*. W. W. Norton and Company, Inc, New York.

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

Linksvayer, T. A. and Wade, M. J. (2005). The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: maternal effects, sibsocial effects, and heterochrony. *Q. Rev. Biol.*, **80**, 317–336.

Maynard Smith, J. and Szathmáry, E. (1995). *The Major Transitions in Evolution*. Oxford University Press, Oxford.

Ratnieks, F. L. W. and Wenseleers, T. (2008). Altruism in insect societies and beyond: voluntary or enforced? *Trends Ecol. Evol.*, **23**, 45–52.

Wolf, J. B., III, E. D. B., Cheverud, J. M., Moore, A. J., and Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.*, **13**, 64–69.