Kinship, Parental Manipulation and Evolutionary Origins of Eusociality

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Introduction

- A eusocial species is one in which large quantities of offspring, in an attempt to help their queen mother produce more siblings, relinquish most or all of their own direct reproductivity.
- The benefit of this alleged altruistic behavior to workers exists *only* if **gains in indirect fitness** associated with raising siblings outweigh the costs, which is often a complete loss of direct fitness.
- Maternal behavior is predicted to play a crucial role in driving the eusocial evolution. This is due to the significant fitness benefits gained by the queens when they succeeded in manipulating their daughters into becoming helpers.
- If the fitness gains for the queen are large enough, maternal manipulation will be sufficient to evolve eusociality despite the lack of net inclusive fitness benefits to workers.

Eusociality

- Division of labor in which...
 - Workers are in charge of foraging
 - Workers feed the queen
 - Workers do not mate
 - Workers do not lay eggs
 - Workers have lower juvenile hormone levels
- Possible evolutionary origins:
 - Maternal Manipulation
 - Worker Altruism







Goals & Hypothesis

- The **goal** of the study was to investigate the ways in which eusociality evolves in natural populations. This was done by measuring the inclusive fitness of the facultatively eusocial sweat bee (*Megalopta genalis*) in order to quantify the direct fitness costs to workers in comparison to the benefits gained by the queens.
- The **hypothesis** was that eusociality may evolve without direct net fitness benefit to workers.

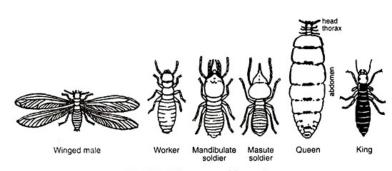


Fig. 5.26: Different castes of the termites



https://www.science.lu.se /article/how-bees-findtheir-way-home

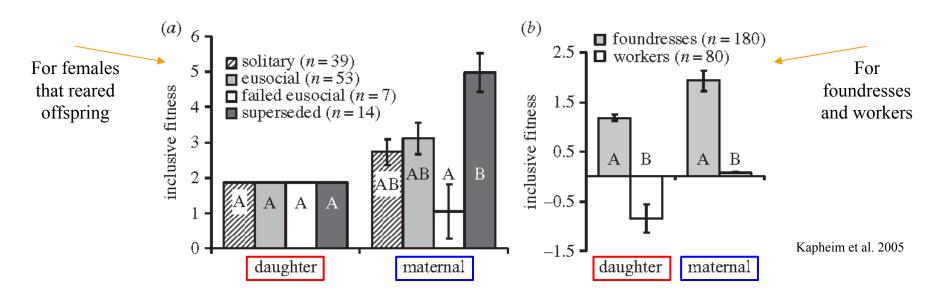
Methods

- In terms of actual field data, **observational nests** were arranged in seven clusters of 10-15 nests each across 1500 ha. Variation, in terms of nest conditions, seasonal effects, and local resource availability, was thus reduced. This was done in order to avoid influence in terms of reproductive success and social behavior.
- Behavioral and genetic data were applied to the **Inclusive Fitness calculations** which were calculated on an individual basis. For each founder and worker, two estimations of Inclusive Fitness were obtained under either one of two assumptions: either the daughter genotype or the foundress genotype are responsible for all social interactions.
- Computer simulations were designed with the intention of creating conditions which give rise to eusocial behaviors using field data. Initially, the likelihood of having either sex offspring is arranged to be 50:50, until sex-biasing alleles are later introduced. In addition, the maternal manipulation begins as a mutant allele which is allowed to spread during the course of the experiment. Data is recorded for 10,000 generations and all simulations are repeated 50 times.

Inclusive Fitness Calculations

- $I_F = (G_n \times r_o) + (G_s \times r_o) + (G_o \times r_r)$
 - \circ G_n = fitness effects of each individual's genotype through nonsocial traits
 - \circ G_s = fitness effects of each individual's genotype through social traits
 - \circ G_0 = fitness effects of each individual's genotype on offspring of others
 - r_o=relatedness to one's own offspring
 - \circ r_r=relatedness to the offspring of those receiving fitness effects

Field Data Results

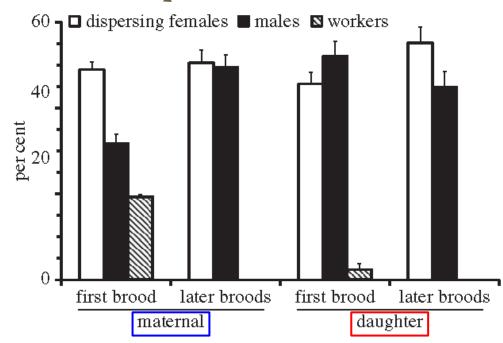


- If eusociality was based on the daughter's genotype, inclusive fitness would be the same regardless of outcome & foundresses would have higher fitness than workers
- If eusociality was based on the mother's genotype, inclusive fitness would be highest for superseded colonies and lowest for failed eusocial & foundresses would have highest fitness

Simulation Model Results

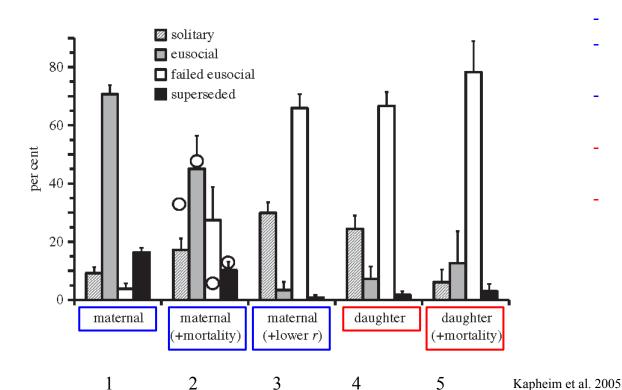
Field data matches maternal

- Maternal genotype: high percentage of workers initially, not later
- Daughter genotype: high numbers of males in first and later broods; lower number of workers



Kapheim et al. 2005

Simulation Model Results



- Maternal: eusocial will prevail
- Maternal w/ increased mortality: eusocial will again prevail
- Maternal w/ less relatedness: failed eusocial is most common
- Daughter: failed eusocial is again most common
- Daughter w/ increased mortality: failed eusocial is again most common

Conclusion

- Eusociality is able to evolve through two methods:
 - o a) parental manipulation
 - o b) worker altruism
- Workers did not significantly increase their inclusive fitness by helping
 - Parental manipulation is needed to encourage eusocial behavior
- When assuming that maternal genotype is in control of social structure, eusociality did not significantly increase inclusive fitness
 - May explain why eusociality is facultative in this species
 - Alternative life histories coexist in this species (eusociality and solitary modes of reproduction)
- Kin selection is important

Discussion

- 1. What were some of the goals of this paper?
- 2. Which evidence did you feel proved the authors' points the best: field data or simulation data? Why?
- 3. Are these findings of the evolutionary mechanisms of eusociality applicable to other species? What are the implications of their findings?
- 4. What did you find to be particular strengths of this paper? What about weaknesses?
- 5. What aspects of this paper could be controversial in the field? Genetic relatedness? Maternal manipulation?
- 6. What are the proximate vs ultimate causes of eusociality?

