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Evolution of Eusociality in Ants Hymenoptera: Formicidae

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**EVOLUTION OF EUSOCIALITY IN ANTS HYMENOPTERA:
FORMICIDAE**

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Abstract

Eusociality can be seen in a variety of insect families, including the ants (Formicidae). There is no clear understanding on how it evolved but it is well understood that transitions between social phases must happen. Several theories and hypothesis have been presented but none of them completely encapsulate the whole evolution of eusociality. Several studies on ants focus on different aspects of their evolution in the eusocial context and provide good supporting data. Two major models, Alternate Inclusive Fitness Model and Worker Behavior Model, are good blueprints for future research. As more data is collected and studies were done, more light will be shed on the subject.

Eusociality

Eusociality is often defined as advance sociality that is characterized by the division of labor between reproductive and non-reproductive caste [1]. This level of sociality evolved in a variety of insect families: Isoptera (Termites), Aphididae (Aphids), Thysanoptera (Thrips), Coleoptera: Scolytidae (Bark Beetles) and Platypodidae (Ambrosia Beetles), as well as Hymenoptera (Sawflies, Wasps, Bees, and Ants) [2]. It has also been used to describe Naked Mole-Rats [3]. By achieving this level of cooperation, new niches can be filled [4]. The question of how eusociality evolved has been a focus of sociobiologists for decades. Several theories have been proposed that target different aspects of evolution. An overarching theme that seems to be agreed on is the idea of transitioning through different levels of sociality. Although terminology varies in literature [2,5–9], the groups are generally defined by the same characteristics. In a recent review of sociality evolution, Rehan and Toth (2015) describe five different levels of sociality on the bases of possessing the three different characteristics (cooperative brood care,

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reproductive division of labor, and overlapping generations) that define eusociality[6]: solitary, subsocial, incipiently social, primitively social, and advanced eusocial. They refer to these levels as “rungs of an evolutionary ladder” which is an easy visual to think about the context of evolution. As the levels become more socially complex, the more eusocial characteristics are obtained. Several researchers theorize that genetics may be the driving force in the selection to become more eusocial[9–16]. Or in other words, these genetic mechanisms are hypothesized to facilitate transitions to a more complex social structure. Specific hypothesis include Ovarian Ground-plan[17], Maternal Heterochrony[12], Genetic Toolkit[11], Novel Genes[18], Protein Evolution[19], and Conserved Regulation[20]. but there are a couple of hypothesis that have been tested in the ant family Formicidae and will be discussed in more detail later.

Some of these transitions have thresholds, eusociality threshold [8] and the ‘point of no return’ i.e. the irreversibility threshold [1,8,10]. The eusociality threshold is marked by allomaternal care and the species is considered to be eusocial. The irreversibility threshold, or as it is often referred to as the point of no return, is marked by the presence of distinct worker castes and discrete queen. After a species reaches this threshold, reversal to a lower level of sociality is almost impossible.

Since the evolution of eusociality has been a highly-studied topic, theories and experiments have been debated and refined across various phylogenetic groups. For this paper, I will focus on eusociality in the ant family Formicidae. All of the species included in this group express some form of eusociality [9]. Because of this, studies about understanding evolutionary paths from primitive sociality to advanced eusociality use the ant phylogeny as an ideal study system. Through reviewing studies done on the ant species, as well as, studies carried out with other eusocial groups, I will provide future avenues for research.

Ant Studies

E. O. Wilson can be considered the one of the first sociobiologists that began the groundwork for the expanding study of evolution of eusociality. His famous book written with Bert Hollidobler, *The Ants*, provides a wide survey of the ant species and different aspects of their biology [21]. This work, along with his earlier work, sparked new ways to understand evolution.

One study carried out by Barbara Thorne and James Traniello focused on the basal groups of ants and termites as a way to understand eusocial behavior in the past [22]. Using the most basal species in both families, inferences were made about ancestral traits based on “primitive” characteristics seen in the extant basal species. It was easy to determine the most basal species to study from genetic phylogenies but inferences on behaviors as “primitive” were used to compile likely traits of extinct lineages during the evolution of eusociality. These traits include reproductive plasticity, division of labor, foraging biology, and evolutionary pathology. Although these groups share a convergent social organization, Hymenoptera species have haplodiploid while Isoptera species are diploid. This means that Hymenoptera are more closely related since sisters share 75% of their genetic DNA while Isoptera are similar to us and share 50% of their genetic DNA with siblings, regardless of sex. It is then hard to compare the two because of the different modes of gene inheritance. As for the division of labor, they say that the disassociation of the food source from the nest led to bigger colonies and thus evolved a working class. This would be supported by the fact that pheromones, temperatures, and nutrition control caste selection. This also supports the idea of worker sterility since they would only develop working reproductive organs if they were introduced to certain pheromones. As for pathology, ants resist infections through their metapleural gland, and in more ancestral species, a

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metapleural gland. Termites do not have this gland due to their bacteria symbionts but may have gained disease resistance through genetic variation. Although this study does present a comparison between the two groups and provides distinct characteristics they were looking for, there still needed to be more comparing from the data presented. Yes, the right questions were asked, but the synthesis wasn't.

In a newer study by Purcell et al. [23], the genome of two species of ants was analyzed and compared between the two social forms in that species. From this, genes that were associated with social organization could be identified. After mapping these genes and finding out they were nonrecombining, comparing the two species showed that the formation of the nonrecombining region is important to the transitions of sociality in ants. They also found that this may have convergently evolved because of the dissimilarity between the species. This is one of the few studies that I found with an in-depth analysis on the genetics of eusociality. As mentioned earlier, a eusocial gene or genes has not been identified yet so comparisons are the best we can do right now.

Looking at another aspect of evolution is a study done on the hypothesis of a colony having a disposable caste [24]. As a defensive strategy, limiting the predation to the low-cost workers would benefit the colony as a whole. *Pogonomyrmex owyheeii* was the species of study and they found that the social structure of the colony allowed for the high predation rate of the foragers. The ants found foraging were old ants that seemed to be at the end of their lifespan and held a small portion of the colony energy. The interior workers on the other hand held most of the energy, where it was safe inside the nest. The need for producing this type of worker drove the formation of polymorphic caste. Although there is no major morphological difference, body

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weight and head appendage wear were defining characteristics of the foraging caste. This study shows yet another selective force that acts on the evolution of eusociality.

The last ant study that I am going to present is testing a hypothesis that deals with the division of labor. The Reproductive Groundplan Hypothesis argues that the cycles controlling reproduction in solitary ancestors were changed to generating division of labor in workers [15]. It also predicts that the use of these cycles still generates allomaternal behaviors. Working castes are expected to have high ovary activation while foraging castes are expected to have low ovary activation. After analyzing data from 64 species, the hypothesis was supported by 92% of the species and the ancestral reconstruction also supported this hypothesis. A functional link in the evolution of ovary activation and castes was also found. Since there is heavy policing of worker reproduction due to the costliness to the colony, this transition would be favored. The researchers also mention that the high energy cost of ovary activation may lead to the foraging class reducing or forgoing ovary activation because of the high mortality rate of foragers. This would reduce the loss of colony energy, as seen in *P. owyheeii* [24].

Major Theories in Eusocial Evolution

The inclusive fitness theory which defines inclusive fitness as the sum of the effect of this action on the actor's own fitness and on the fitness of the recipient multiplied by the relatedness between actor and recipient, where 'recipient' refers to anyone whose fitness is modified by the action [14].” This is derived from Hamilton's rule of altruism inequality, $R > c/b$, where the behavior is favored if the relatedness is greater than the cost/benefit ratio [25]. This would be supported by the haploiddiploid sex configuration found in Hymenoptera [14]. However, it was stated that other eusocial groups don't follow this sex configuration, i.e. termites. They describe

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two reasons why this theory is limited: 1) inclusive fitness theory requires additive and pairwise interactions. 2) only works with special population structures, such as static or dynamic. Also it is mentioned that empirical studies lack complete measurements of each quantity in the formula. The alternate theory they provide has five steps in the origin of eusociality. First, group formation in freely mixing populations. Groups will form when cooperation between unrelated individuals is beneficial, such as defense of a nest or food provisioning. Second, accumulation of traits leading to eusociality, i.e. preadaptations. Third, evolution of eusocial genes through mutation or recombination. The behaviors gained by these groups would act on the selection of these genes. Fourth, the study of population genetics and behavioral ecology. Environmental selective forces help shape the evolution of eusociality. Fifth, selection of colony traits, seen in advanced eusocial species. This article provides a great outline on the study of how eusociality evolved. More importantly, it points out the faults

and lack of studies done in important aspects of evolution. Basic evolutionary knowledge tells us that phenotypes are acted on by outside factors and change the genotypes of an individual.

A comparative study done on the wasp family Vespidae provides an excellent model on the origin of worker behavior and it's relation to eusociality evolution. By including the different levels of eusociality, the transitions between levels, the thresholds, and changes in worker behavior, this model provides a holistic view on how behaviors

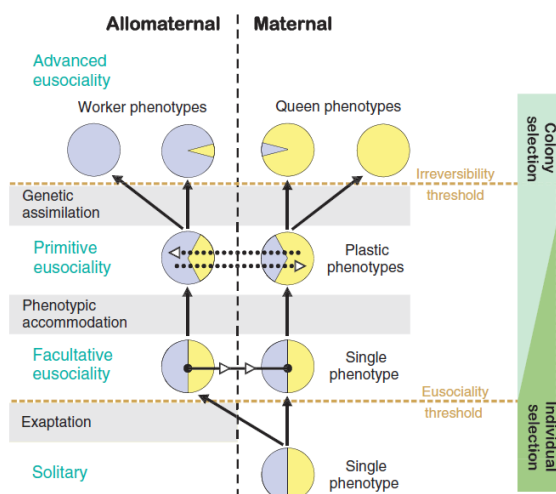


Fig. 1 Allomaternal and Maternal worker behavior are divided with the vertical dotted line. Circles represent maternal behavior (dark color = foraging, larval care, nest construction; light color = ovary activity, oviposition). Solid horizontal arrows show transition to maternal. Dotted horizontal arrows show possible transitions. Gray bars represent transition between eusocial levels. The vertical bar shows what selection acts on. The horizontal dotted lines represent the thresholds of eusociality. [8] (figure taken from Hunt 2011)

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evolved with eusociality. Previous studies of wasp found that a “plasticity first, genes as followers” [8], made allele-based models inefficient in understanding the eusociality origin.

More empirical research can be done based on this model to focus future research. Although this only includes worker behavior, it provides a start for better understanding research being done.

Where do we go from here?

There have already been numerous studies conducted on the eusocial behavior in ants and other species. However, there does not seem to be a focus on a general theory of eusocial evolution in ants. The studies I discussed, as well as many others, provide evidence on only a fraction of the problem and disregard the complete idea of eusocial evolution. Because of how many different parts can make up how a trait evolves, having similar studies conducted across several different eusocial groups would provide a much-needed comparison between Hymoptera and other eusocial organisms. The model on worker behavior would be a good start to this dilemma. Using the same methods used in that study, comparisons across groups would maybe open up new ideas or areas for research that would even further our idea of evolution in eusociality. Personally, I would be interested in doing graduate research in this subject, not only to further my knowledge but also to be able to contribute to this fascinating debate. As the debate goes on, more data will only help clarify for disprove current theories and ideas. In order to narrow down the focus of future research, I will propose questions to be studied.

Future Research Questions

1. How do the genomes of closely related species in different levels of sociality compare?
2. Can the Worker Behavior Model be used with Formicidae?
3. Why do juveniles develop the altruistic trait? [8]

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