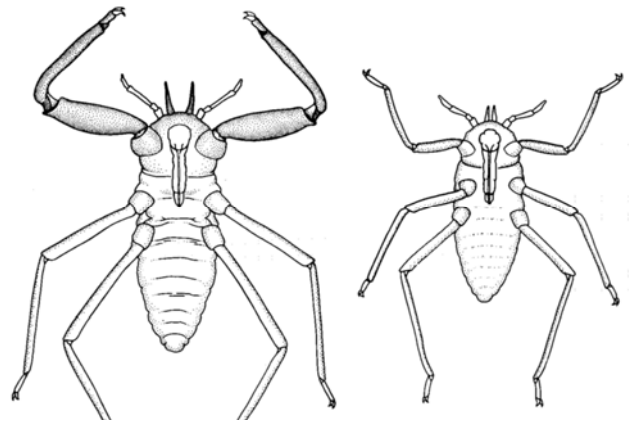


## 12: Social Insects

### What can lead to the evolution of sociality? An example...

Some aphids in the subfamilies Pemphiginae and Hormaphidinae (Hemiptera: Aphididae) have a sacrificial soldier caste. Some first and second-instar nymphs exhibit aggressive behavior and defend their sisters from competition and harm. These nymphs never develop into adults and never reproduce. Instead, they develop a different morphology than their sisters with more sclerotized body parts and big, muscular front legs. They attack intruders with frontal horns or their piercing mouthparts. Image: the one on the left is the soldier. Note the hefty front legs and their frontal horns.



Why such altruism? Why are these nymphs sacrificing themselves to protect other aphids?

The soldiers are genetically identical to their sisters, and so they have increased **inclusive fitness** via **kin selection** when they defend their family against predators. Thus, the differences between the two types of sisters is due to **phenotypic plasticity** (different phenotypes, same genotypes).

**A tangent on parthenogenesis.** Many aphids reproduce through **parthenogenesis**, which is development from an unfertilized egg. Growth and development of embryos occur without fertilization by a male. **Parthenogenesis** is one form of asexual reproduction. The word "parthenogenesis" comes from the Greek παρθένος, parthenos, meaning "virgin", and γένεσις, genesis, meaning "birth". Parthenogenic offspring usually are diploid. Usually, meiosis occurs, creating haploid eggs. The chromosome number of the haploid egg cell can be doubled during development, making the offspring "half a clone" of its mother. If the egg cell was formed without meiosis, the offspring will be a full clone of its mother. Similarly, parthenogenic offspring are sometimes clones of their sisters, which brings us back to the aphids...

Soldiers and normal nymph aphids are genetically identical, and this situation has favored the evolution of altruistic soldiers. A similar phenomenon occurs in related aphid species, but they have nymphs that are only temporary soldiers that later molt into normal, non-aggressive individuals that reproduce. The unusual aphid polyphenism has led some researchers to argue that Hemiptera is a third insect order displaying **eusociality**, but these aphids do not fit the other characteristics of true eusocial insects. Hence, these aphids are considered to be **subsocial**.

## Eusocial and Subsocial Insects

Eusociality is defined by three traits. Eusocial insects exhibit **all three** of the following:

- 1) Cooperative Brood Care
- 2) Overlap of generations
- 3) Reproductive division of labor

Eusociality occurs in all ants, termites, and some bees and wasps. Subsociality is much more widespread and known to have arisen independently in 13 orders of insects, including some cockroaches, embiopterans, thysanopterans, hemipterans, coleopterans, and hymenopterans.

## Subsociality

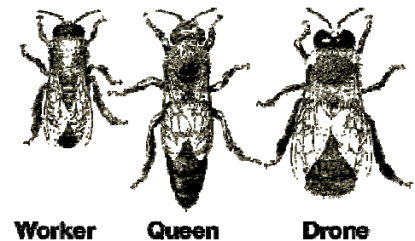
Subsocial insects include all of those that exhibit **at least one** social characteristic. They may:

- Aggregate
- Has a division of labor (e.g. soldier castes)
- Cares for eggs or young after the eggs are laid



## Eusociality

Eusocial insects have a division of labor in their colonies, which includes a caste system. The reproductive females are called **queens** (also called **gynes**), and they are aided by **workers**. Workers are non-reproductive individuals that help the reproducers. In termites and many ants, an additional defensive **soldier** caste is also produced. There may be additional subcastes that perform specific tasks as well. Often queens and soldiers are so highly specialized at their work that they cannot feed themselves. Workers may bring food to these individuals as well as to the **brood**, the developing offspring. Illustration above: honey bee castes.



Eusocial Hymenoptera have a **haplodiploid** genetic system where queens control the sex of their offspring. If they release stored sperm to fertilize haploid eggs, that will result in diploid female offspring. Unfertilized eggs result in male offspring. In the eusocial Hymenoptera, males are often rare, and live only to reproduce and die. Winged male and female reproductive are called **alates**. In termites, males and females may be equally represented, with both sexes serving as members of the worker caste. A single male termite, the **king**, permanently resides with the **gyne**.

Members of different castes may be genetically identical or at least related. However, they can be morphologically very distinct. This is an example of **polyphenism**, as described above with the aphids.



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Bumble bees (Hymenoptera: Apidae) are considered to be **primitively eusocial**. They found colonies through a single queen, often following a fight to the death between females vying for a good nest site. The first brood consists of workers only and they are dominated by the queen physically. The queen is aggressive and will eat any worker eggs and use pheromones to modify worker behavior. Later in the season the queen's physical and chemical influence over the workers diminishes, and workers begin to undergo ovarian development. The workers eventually defeat the queen,

killing her or driving her away. When this happens, workers are unmated, but they can produce male offspring from their haploid eggs. Thus, female bumblebees only come from queen bees.

Insects with **specialized eusociality** include those species with highly specialized castes. The queen is generally larger than the workers and may have an enlarged abdomen. Workers will have different morphological structures, e.g. worker honeybees have wax glands and a pollen-collecting apparatus.

## Evolution of Eusociality

The principle of **kin selection** starts by recognizing that **classical** or **Darwinian fitness** (the number of offspring that survive to reproduce) is only part of the contribution to an individual's total or **inclusive fitness**. There is an additional indirect contribution, termed the kinship component. This is the fitness gained by helping relatives (kin). Kin are individuals with similar or identical genotypes. In the Hymenoptera, kind relatedness is enhanced by the haplodiploid genetic system. In fact, eusociality has independently evolved many times in hymenopterans. Because males are haploid, each sperm (produced by mitosis) contains 100% of the dad's genes. In contrast, the egg (produced by meiosis) is diploid, and only half of the genes are from the mom. Thus, daughters, produced by fertilized eggs, share all their father's genes, but only half of their mother's genes. Further, full sisters (with the same father) share 75% of their genes on average. Therefore, sisters share more genes with each other than they would with their own female offspring (50%). Thus, the inclusive fitness of a sterile female worker is greater than her classical fitness. A worker should invest in the survival of her sisters, the queen's offspring, rather than in the production of her own female young.

Hamilton's Rule:

$$rB - C > 0$$

Emphasizes the costs and benefits involved with altruistic behavior.  $r$  is the coefficient of relatedness,  $B$  is the benefit gained by the recipient of altruism, and  $C$  is the cost suffered by the donor of altruism. For altruism, and eventually eusociality, to evolve, Hamilton's Rule must be true.

# Eusociality in Termites

In contrast to the haplodiploidy of Hymenoptera, termite sex is determined universally by an XX/XY chromosome system. There is, therefore, no genetic predisposition towards kinship-based eusociality. So, termites present a real puzzle: why are they eusocial? Wouldn't it be better for termites to strike out on their own and focus on their own reproduction?



A leading hypothesis for the evolution of eusociality in termites focuses on the nutrient-poor food source and the longevity of adults. Termites need to transfer **symbionts** to be able to digest wood. High levels of intracolony interaction help the termites gain the needed symbionts to tolerate their nutrient-poor food source. A particular behavior, called **trophallaxis**, is used to transfer symbionts. This involves mouth-to-mouth or mouth-to-anus contact. Termites also need overlapping generations to be able to pass on these symbionts.

## Maintenance of the eusocial colony



As discussed above, workers social hymenopterans give up their chance to reproduce and raise their sisters instead. This system depends upon kinship to provide **inclusive fitness**. However, occasionally all is not peaceful and orderly within eusocial colonies. Workers sometimes try to sneak in eggs of their own with the brood. Other workers may serve as a “police force” and actually eat the eggs of the other sneaky workers. Such behaviors have been seen in honey bees, some wasps, and some ants. For example, in a typical honey-bee colony of 30,000 workers, on average only three have functioning ovaries. These three workers can be responsible for up to 7% of the

male eggs laid. Many of such eggs are eaten, so that only 0.1% of the males emerging from a colony had a worker as a mother.

## Success of the eusocial insects

Eusocial insects can be extremely abundant in some areas, especially in the tropics and at low latitudes. Three qualities of eusocial insects are thought to contribute to their competitive advantage, and all are related to the caste system that allows multiple tasks to be performed by different individuals.

- 1) Many different tasks can be performed simultaneously by different groups. One activity does not jeopardize another, thus, for example, the nest is not vulnerable to predators or parasites while foraging is taking place.
- 2) Their unity can lead to accomplishments not possible when single individuals work alone, e.g. group defense against large predators or construction of huge nests.

- 3) Homostatic regulation. For example, they can a) regulate and store their food and b) control the microclimate in their nest (e.g. honey bees flap their wings together to cool hives).

## **13: Social Insects**

### **Study Questions & Objectives**

- Name the genetic sex-determination system that has predisposed hymenopterans to evolve eusociality. Is a worker more closely related to her own daughter or her sister? Why?
- List three potential costs of being social
- Some aphids in the subfamilies Pemphiginae and Hormaphidinae (Hemiptera: Aphididae) have a sacrificial soldier caste. Use this example to explain **kin selection** and **inclusive fitness**.
- Explain what classifies an insect as subsocial.
- What is the leading hypothesis explaining why eusociality has evolved in species (such as termites and naked mole rats) without a haplodiploid genetic system?
- List the three qualities of eusocial insects that are thought to contribute to their competitive advantage in ecosystems.

### **Study Questions & Objectives from *Life in the Undergrowth: Super Societies***

- How do bumblebee queens and their daughters interact over the course of a season? See course packet and “Supersocieties” video (part of Life in the Undergrowth DVD)
- Explain the competitive relationship between night ants and harvester ants. How do night ants slow down their rival? (from “Supersocieties” video, part of Life in the Undergrowth DVD)
- Where do the termite-eating ants sting the termites? Why don't they kill the entire colony of termites? ? (from “Supersocieties” video, part of Life in the Undergrowth DVD)
- Describe something else from this video that you found interesting and link it to study terms used in the class.

### **Study Terms**

Eusociality, Sub-sociality, Solitary insects

Queens, Workers, Soldiers, Gynes, Drones

Alates

Haplodiploidy

Symbionts, polyphenism

Classical or Darwinian fitness

Parthenogenesis

Kin selection, Inclusive fitness, Altruism, Parthenogenesis

