"Testing the Kin Selection Theory: Who Controls the Investments?" from The Ants (1990), by Bert Hölldobler and Edward O. Wilson [1]

By: Dhein, Kelle Keywords: Social Behavior [2]

In "Testing the Kin Selection Theory: Who Controls the Investments?" Bert Hölldobler and Edward Osborne Wilson discussed the predictive power of kin selection theory, a theory about the evolution [3] of social behaviors. As part of Hölldobler and Wilson's 1990 book titled *The Ants*, Hölldobler and Wilson compared predictions about the reproductive practices of ants to data about the reproductive practices of ants. They showed that the data generally supported the expected behaviors proposed by kin selection theory. Later in their careers, both Hölldobler and Wilson argued that kin selection theory provided an insufficient explanation for the evolution [3] of social behavior. Hölldobler and Wilsons' efforts were emblematic of a larger trend among ant researchers and sociobiologists to explain the evolution [3] of social behavior by focusing on the reproductive dynamics of social organisms.

Hölldobler and Wilson met in 1969 at Harvard University [4] in Cambridge, Massachusetts, where Wilson was a professor of zoology and Hölldobler was a visiting scholar. In 1971, Hölldobler returned to the Universität Würzburg (University of Wurzburg) in Würzburg, Germany, but he accepted a full professorship at Harvard University [4] in 1973. In the following years, Hölldobler and Wilson collaborated on ant research, eventually writing the 1990 book *The Ants*, a comprehensive survey of ant anatomy, physiology, behavior, and phylogeny [5]. Hölldobler and Wilson's study of kin selection theory appears in the fourth chapter of *The Ants*, "Altruism and the Origin of the Worker Caste," in which Hölldobler and Wilson investigate the evolutionary origins of the worker caste in ants.

Worker ants are distinguished from the rest of the ants in an ant colony by their limited ability to reproduce. Most of the ants in a colony are worker ants. Worker ants are always female, often sterile, and provide most of the labor necessary to sustain an ant colony. Reproductively active ants, or fertile ants that are specialized for reproduction, include female queen ants and male ants. According to Hölldobler and Wilson, worker ants represent a peculiar problem for evolutionary theorists because the behavior of worker ants seems to conflict with then current theories about natural selection [6].

As Hölldobler and Wilson explain in the passages preceding "Testing the Kin Selection Theory: Who Controls the Investments?" evolutionary theorists sometimes use the metaphor of selfishness to explain how genes [7] persist across generations of organisms. Hölldobler and Wilson describe how evolutionary theorists describe genes [7] as selfish because genes [7] persist in a population at the expense of other genes [7] and because they lead their host organisms to reproduce. If genes [7] are selfish, Hölldobler and Wilson argue, then the behavior of worker ants requires a special explanation as the genes [7] of worker ants do not lead them to reproduce.

In their search for an evolutionary explanation of worker ant behavior, Hölldobler and Wilson evaluated a theory called kin selection theory, which explains how a worker ant's behavior affects her relative's ability to reproduce. When a worker ant exhibits social behavior that helps her relative reproduce, then the worker ant shares genetic material with her relative that can still be transmitted to future generations through the reproductive activity of that relative. For example, if a worker ant sacrifices herself to save her sister and that sister goes on to produce offspring, then the worker ant's genetic material, which she shares with her sister, may be transmitted via her sister to her sister's offspring. According to Hölldobler and Wilson, kin selection theory holds that worker ants work for the benefit of their colony without reproducing because worker ants have their reproductively active relatives to reproduce for them. However, kin selection theory makes no claims about how ants experience the world. Rather, the theory attempts to explain how worker ant behavior evolves.

Hölldobler and Wilson tested kin selection theory by comparing kin selection theorists' predictions about the reproductive practices of ants with published data on the reproductive practices of ants. More specifically, Hölldobler and Wilson compared the predicted and observed sex ratios of reproductively active ants in various kinds of ant colonies. For the purposes of Hölldobler and Wilson's evaluation, the sex ratio of an ant population describes the combined weight of female ants relative to the combined weight of male ants in that population. If the sex ratio of a group of ants were three to one, for instance, there would be three grams of female ant for every one gram of male ant.

Hölldobler and Wilson tested the predictions forwarded by kin selection theorists Robert Trivers and Hope Hare in the 1976 paper, "Haplodiploidy and the Evolution of the Social Insects." At Harvard University [4], Trivers and Hare hypothesized that worker ants behave in a way that favors the reproductive success of those most closely related to them. Because the degree of relatedness between workers, male reproductive ants, and female reproductive ants varies according to colony type, Trivers and Hare categorized their predictions of annual sex ratios of reproductively active ants by different types of colonies, not different species of ants.

Hölldobler and Wilson focused on the predictions Trivers and Hare made about three different types of colonies: colonies containing a single egg [8] laying queen, colonies containing multiple egg [8] laying queens, and mixed colonies, or colonies containing one or more parasitic queens. Parasitic queens survive and reproduce by entering established ant colonies, benefiting from the colony's resources, and in some cases killing the original queen.

The first type of colony Hölldobler and Wilson examined were single queen colonies. In ant colonies with one queen, Trivers and Hare predicted a three to one sex ratio in favor of females. Hölldobler and Wilson looked at then current data on the observed sex ratio of reproductive ants produced by single queen colonies across various ant species and found

that the data supported Trivers and Hare's predicted three to one sex ratio. The data referenced by Hölldobler and Wilson held that male reproductive ants comprised approximately twenty-eight percent of the total weight of the reproductive ants produced by a single queen.

The second type of colony Hölldobler and Wilson examined were colonies containing multiple queens. For multi-queen colonies, Trivers and Hare predicted a one to one sex ratio. Comparing that prediction to published data on the sex ratio of reproductive ants produced by multi-queen colonies, Hölldobler and Wilson found that the data supported a one to one sex ratio. In multi-queen colonies, researchers found that approximately fifty-two percent of the total mass of reproductive ants were male ants.

For the third and final type of colony, Hölldobler and Wilson examined mixed colonies in which there were one or more parasitic queens extracting resources from a host colony. Like in multi-queen colonies, Trivers and Hare predicted a one to one sex ratio, which empirical data confirmed. Hölldobler and Wilson examined data showing that male reproductive ants comprised approximately fifty-two percent of the combined weight of reproductive ants produced by mixed colonies.

Having compared predicted sex ratios with the observed sex ratios of reproductive ants from three different types of colonies, Hölldobler and Wilson conclude that empirical data confirmed kin selection theory as an explanation of how worker ant castes and behavior evolved.

After presenting evidence in favor of kin selection theory in "Testing the Kin Selection Theory: Who Controls the Investments?" Hölldobler and Wilson continued to publish on the topic into the twenty-first century. In 2005, they presented another theory, called group selection theory, as a more prominent factor than kin selection theory in the evolution [3] of social insects [9]. Both group selection theory and kin selection theory offer explanations for how organisms evolve social behaviors, but group selection theory hypothesizes that groups of organisms, not specific genes [7], drive the evolution [3] of sociality. By 2016, group selection theory remained controversial in the field of evolutionary biology.

In "Testing the Kin Selection Theory: Who Controls the Investments," the experimental data on sex ratios among reproductive ants provided ant researchers with a clear, comprehensive data set on an important phenomenon in the reproductive life cycle of ants. Hölldobler and Wilson's testing of kin selection theory also contributed to a larger debate about how organisms develop and retain social traits.

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Subject

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