”Altruism and the Origin of the Worker Caste” from The Ants (1990), by Bert Hölldobler and Edward Osborne Wilson

In ”Altruism and the Origin of the Worker Caste,” Bert Hölldobler and Edward Osborne Wilson explore the evolutionary origins of worker ants. ”Altruism and the Origin of the Worker Caste” is the fourth chapter of Hölldobler and Wilson's book, The Ants, which was published by The Belknap Press of Harvard University in Cambridge, Massachusetts, in 1990. In ”Altruism and the Origin of the Worker Caste,” Hölldobler and Wilson evaluate various explanations for how a non-reproductive caste of ant evolved. Their investigation into the evolutionary origins of worker ants synthesized research on the reproductive practices of ants to provide an analysis of how sterile groups of organisms persist in a population.

Hölldobler and Wilson first met in 1969 at Harvard University in Cambridge, Massachusetts, where Hölldobler researched ants as a visiting scholar. Wilson, also an ant researcher, was Hölldobler's host at the university. The two began eating lunch together and talking about their shared interests in social insects, insects that live in cooperative colonies composed of multiple generations. Hölldobler accepted a professorship at Harvard University in 1973, and he and Wilson began collaborating on a series of academic articles concerning ants. Around 1986, Hölldobler reported that he and Wilson began writing their comprehensive book titled, The Ants.

The Ants aims to provide a review of the academic literature on ants as of 1990, the year the book was published. The Ants is 732 pages long and contains many photos and illustrations of ants. ”Altruism and the Origin of the Worker Caste” is the fourth chapter of The Ants. The chapter includes four black and white photos of ants, eight data visualizations, and is seventeen pages long.

”Altruism and the Origin of the Worker Caste” is subdivided into six sections titled ”Altruism,” ”Kin Selection,” ”Parental Manipulation,” ”Offspring Consent,” ”Testing the Kin Selection Theory,” ”Eusociality and Chromosome Numbers,” and ”Overview”.

In the first section, ”Altruism,” Hölldobler and Wilson argue that the existence of worker ants requires a different kind of evolutionary explanation than does existence of most other kinds of organisms. Most ant colonies contain two distinct ant castes, or divisions of roles: workers and reproductives. Worker ants perform most of the tasks necessary to sustain an ant colony, such as finding food, maintaining the colony infrastructure, and protecting against predators. Though the behavioral and physical characteristics of worker ants vary by to species, worker ants all do not reproduce and are often completely sterile Reproductive ants, by contrast, nearly exclusively focus on the work of reproduction and make up a much smaller proportion of the ant colony. Because worker ants do not reproduce, they do not pass their genes on to any offspring, so they are outside traditional theories of evolution by natural selection. Hölldobler and Wilson begin their argument for the peculiarity of worker ants by noting that according to a modern conception of natural selection, genes are selfish. When Hölldobler and Wilson say that genes are selfish, they are not saying that genes have intentions or other mental states. Rather, genes are selfish because they lead to behavior that facilitates their transmission to future generations through reproduction. In other words, a gene persists in a population at the expense of other genes. Worker ants present a peculiar case in the evolution of life, Hölldobler and Wilson argue, because their selfish genes have somehow led to seemingly unselfish behavior. Worker ants provide valuable services that help their nest mates reproduce without reproducing themselves.

To motivate their claim that worker ants exhibit unselfish behavior, Hölldobler and Wilson note that the worker ants of most species do not attempt to reproduce, that worker ants often perform dangerous work for the benefit of their nest mates, and that the worker ants of some ant species defend their nests to the death. Worker ants of the Camponotus saundersi species, for example, employ a suicidal defense mechanism in which they contract their abdomens until their body walls burst, discharging large amounts of sticky fluid that immobilize attackers. Such acts of suicidal nest defense seem selfless from an evolutionary point of view because the defending ant is protecting her nest mates at the cost of forfeiting her ability pass on her own genes through reproduction. To explain the evolutionary development of such selfless behavior, Hölldobler and Wilson examine three theories that ant researchers have proposed.

In the ”Kin Selection” section, Hölldobler and Wilson examine the proposed evolutionary explanations of kin selection theory. Kin selection theory seeks to explain the selfless behavior of worker ants by tracing the genetic consequences of that selfless behavior. Though an apparently selfless act may preclude a worker from transmitting her genes through reproduction, kin selection theory holds that selfless acts can still cause some of the worker's genes to be transmitted to the next generation of offspring. Those genes transmit if the selfless act makes reproduction more likely for the worker's close relatives, who likely share some of the worker's genes. Because the seemingly selfless act helps transmit some of the worker's genes, although indirectly, to the next generation, the act provides some reproductive benefit to the worker as well.

To explain how the selfless behavior of worker ants might have evolved given kin selection theory, Hölldobler and Wilson provide a brief thought experiment in the ”Kin Selection” section of the chapter. Hölldobler and Wilson ask the reader to imagine that a gene appears in a population that causes its bearer to triple the reproduction rate of her sister. Instead of producing one offspring a year, the sister produces three offspring a year. Now suppose that that gene also causes its bearer to sacrifice herself in the process of tripling her sister's reproduction rate. As long as that gene appears not only in the dead gene bearer, but also in the gene bearer's sister, the gene can continue to spread through the population. The gene can continue to spread through the population because the sister can now produce three times as many offspring as she could before the gene bearer sacrificed herself, and all of the sister's offspring will inherit the gene. Thus, it is possible for a gene leading to selfless behavior, such as self-sacrifice, to persist in a population so long as the beneficiary of that selfless behavior also possesses and passes on the same gene. Applying the thought experiment to worker ants, proponents of kin selection theory argue that worker ants persist because their selfless behavior helps relatives that share their genes to reproduce.

While explaining kin selection theory, Hölldobler and Wilson trace the theory's history from its rough formulation by the nineteenth century naturalist Charles Darwin to its formulation as a genetic theory largely developed by the twentieth century evolutionary biologist William Donald Hamilton. In tracing the history of kin selection theory, Hölldobler and Wilson include many of the mathematical models developed and inspired by Hamilton. Hamilton's models try to describe the environmental and genetic conditions under which genes prescribing unselfish behavior might spread within a population.

After explaining kin selection theory, Hölldobler and Wilson discuss a second theory called mutualism. Mutualism proposes that cooperation can evolve when a group of individuals are more reproductively successful than a single individual would have been under the same conditions. Reproductive success is a measure of the number of times an individual reproduces in her lifetime. The more times an individual reproduces, the more reproductively successful that individual is. According to mutualism, each organism in a cooperating group must increase its reproductive success as a consequence of belonging to that group. Supporters of mutualism claim that ancestral ants began cooperating because individuals were more reproductively successful in groups than on their own. Though Hölldobler and Wilson acknowledge that mutualism provides a possible explanation for the origin of insect societies, they argue that mutualism cannot fully explain the origin of the worker caste in ants because worker ants are often sterile, and therefore cannot increase their reproductive success by cooperating within a group.

Finally, Hölldobler and Wilson consider another theory for the evolution of worker ants called parental manipulation theory in the ”Parental Manipulation” section of the chapter. According to parental manipulation theory, the worker caste arose as a consequence of female ants attempting to increase their own reproductive success at the expense of their offspring's reproductive success. Hölldobler and Wilson explain that the major premise of parental manipulation theory, as applied to ants, is that mother ants are more related to their offspring than they are to their grandchildren. Whereas a mother ant is likely to share half of her genes with her daughter, that same mother ant is likely to share only a quarter of her genes with her granddaughter. Thus, it is in the mother's reproductive interest to force some of her offspring to forgo reproduction so long as the offspring's forgoing of reproduction helps the mother become more reproductively successful. By forcing some of her offspring to forego reproduction, and instead maintain and defend the nest, collect resources, and raise their siblings, the mother forgoes future grandchildren for more of her own offspring. Those offspring will be more genetically similar to the mother ant than her grandchildren would have been, thereby increasing the likelihood that the mother's genes persist in future generations. Of the three theories surveyed in "Altruism and the Origin of the Worker Caste," Hölldobler and Wilson give the most support to kin selection theory and parental manipulation theory.

Having surveyed three major theories for the origin of the worker caste, Hölldobler and Wilson spend the next section of the chapter, titled "Offspring Consent," explaining why kin selection theory is a more falsifiable, and therefore better, scientific theory than parental manipulation theory. When Hölldobler and Wilson write that kinship selection theory is more falsifiable than parental manipulation theory, they mean that kin selection theory makes more testable predictions than does parental manipulation theory. In other words, kin selection theory, makes predictions about current ant populations that can be tested to produce experimental evidence that support or reject kin selection theory. Parental manipulation theory, on the other hand, is less falsifiable because it makes predictions about the behavior of ancestral ants that can no longer be observed.

Hölldobler and Wilson explain in the final half of "Offspring Consent" that kin selection theory yields testable predictions about current ant populations because of an unusual feature of ant reproduction. That feature is the haplodiploid method of sex determination that all ant species exhibit. Most organisms are diploid, meaning that both male and female individuals inherit paired sets of chromosomes, one half of each pair from their mother and the other half from their father. In haplodiploid organisms such as ants, males develop from unfertilized eggs, meaning that they inherit chromosomes exclusively from their mother, and are therefore haploid, possessing an unpaired set of chromosomes. Female ants, on the other hand, are diploid, possessing a full, paired set of chromosomes. They develop from fertilized eggs and inherit half of their chromosomes from their mother and half from their father.

Hölldobler and Wilson argue at the end of "Offspring Consent" that the haplodiploid method of sex determination enables researchers to test kin selection theory, because haplodiploidy causes closely related individuals to have very different combinations of genes. Because male ants are haploid, Hölldobler and Wilson explain, they produce genetically uniform male reproductive cells, meaning that all of a father's daughters will share all of the father's genetic material. Compared to other diploid organisms like mammals, female ants are more closely related to their sisters, the share more of the same genes. Because daughter ants inherit all of their father's genetic material, daughter ants are likely to share, on average, three fourths of their genetic material with their sisters, half of the genetic material from their mother and all from their father. At the same time, daughter ants only share half of their genetic material with their mother.

Hölldobler and Wilson argue that such asymmetries enable ant researchers to use kin selection theory make testable predictions that the seemingly selfless behavior of worker ants result from the amount of genetic relatedness between worker ants and the rest of the colony. Ant researchers, Hölldobler and Wilson argue, can test kin selection theory by discovering whether or not worker ants behave in a way that favors the reproductive success of those nest mates most closely related to the workers. Hölldobler and Wilson include a figure in the "Offspring Consent" section of the chapter which details the degrees of relatedness among all members of an ant colony.

In the fifth and longest section of the chapter, "Testing the Kin Selection Theory," Hölldobler and Wilson weigh the explanatory merits of kin selection theory by comparing the predictions kin selection theory makes with experimental data. Hölldobler and Wilson organize "Testing the Kin Selection Theory" into a series of questions. They first pose a question, consider what the answer would be given kin selection theory, and then interpret experimental data to determine whether or not those data support the answer predicted by kin selection theory.

The first question Hölldobler and Wilson consider is: what types of insects have evolved eusociality? Eusocial insects, Hölldobler and Wilson explain, are distinguished by three traits. First, eusocial insects are divided into reproductive and sterile castes. In ants, workers, which are always female, constitute the sterile caste, while reproductive females, called queens, and males constitute the reproductive caste. The second distinguishing trait of eusocial insects, as defined by Hölldobler and Wilson, is that the sterile caste cooperates to raise the young of the reproductive caste. Finally, the third distinguishing trait of eusocial insects is that their cooperative groups contain multiple generations.

For the first question, Hölldobler and Wilson argue that, given kin selection theory, researchers should expect eusociality to be more common in haplodiploid insects than in diploid insects. Hölldobler and Wilson argue that haplodiploid insects should be more likely to evolve eusocial traits because haplodiploidy causes sisters to be more closely related to each other. As a result, sterile females will be able to pass on more of their genes by helping their non-sterile sisters reproduce under a haplodiploid reproductive scheme than they would under a diploid reproductive scheme. Considering the observational data, Hölldobler and Wilson conclude that the predictions of kin selection theory align with experimental observations. Eusociality is much more common among haplodiploid insects, such as ants, wasps, and bees, than among diploid insects. In fact, Hölldobler and Wilson note that termites are the only known instance of eusociality in a diploid insect species.

The second question Hölldobler and Wilson consider in ”Testing the Kin Selection Theory” is: are worker ants ever male? Based on kin selection theory, Hölldobler and Wilson argue that no worker ant should be male. Hölldobler and Wilson state that ant researchers should expect worker ants to be universally female because, as deduced by the late twentieth century entomologist Stephen Bartz, the asymmetries in genetic similarity caused by haplodiploidy combined with the assumptions of kin selection theory suggest that a uniformly female caste of sterile workers the most reproductively advantageous option for a queen. Once again, Hölldobler and Wilson find that empirical evidence supports the prediction made by kin selection theory. In every observed ant species, the worker caste is exclusively female.

Hölldobler and Wilson continue ”Testing the Kin Selection Theory” with a third question: how closely related are the ants of a single colony? If kin selection theory is correct, Hölldobler and Wilson claim that worker ants should be at least as related to their reproductively active siblings as they would have been to their offspring, had the worker ants reproduced themselves. They explain that according to kin selection theory, the workers' reproductively active siblings fulfill the role that would have been played by the workers' offspring. Instead of relying on their offspring to transmit their genetic material by producing grandchildren, kin selection theory predicts that worker ants rely on their reproductive siblings to transmit their genetic material by producing nieces and nephews. If a worker's reproductively active siblings are at least as related to the worker as that worker's offspring would have been, then the nieces and nephews of the worker's reproductive sibling will tend to carry at least as much of the worker's genetic material as the worker's grandchildren would have.

To answer that third question, Hölldobler and Wilson construct a table synthesizing experimental data on the degrees of genetic relatedness within various ant populations. The table includes data from thirty different ant colonies spanning eleven different species. Besides listing the degree of genetic relatedness between colony members, the table also includes information about the researchers who produced the data, the methods those researchers used to obtain their data, and the number of queens observed in each colony.

After examining the data, Hölldobler and Wilson argue that the degrees of relatedness observed in ant colonies housing multiple queens present a problem for kin selection theory. Though kin selection theory predicts that worker ants should be at least as related to the males and queens produced by their colony as they would have been to their own offspring, Hölldobler and Wilson find that worker ants in multi-queen colonies are less related to their reproductively active siblings than they would have been to their own offspring, had the worker ants reproduced themselves.

Hölldobler and Wilson argue that the observed degrees of relatedness within multi-queen colonies may be a major problem for kin selection theory because there is evidence that ancestral ants developed eusocial traits while living in colonies with multiple, not single, queens. They explain that the problem is that although kin selection theory stipulates a certain level genetic relatedness within a colony as a prerequisite for the development of the worker caste, the data indicates that many ant species with a worker caste lack the degree of genetic relatedness predicted by kin selection theory. Hölldobler and Wilson conclude that observational data does not support kin selection theory's answer to their third question.

Further evaluating kin selection theory in ”Testing the Kin Selection Theory,” Hölldobler and Wilson consider a fourth question: who lays the eggs? If kin selection theory is correct, then workers should help closely related siblings reproduce rather than reproduce themselves. In most ant species, queen ants are the primary egg layers, but worker ants sometimes lay eggs, too. In the cases in which worker ants lay eggs, Hölldobler and Wilson find that workers tend to produce a marginal amount of eggs relative to the colony's total output, and that workers are almost always inhibited from laying eggs by the queen ant of a colony.

Hölldobler and Wilson interpret the fact that queen ants inhibit worker ants from laying eggs as support for parental manipulation theory over kin selection theory. Worker ants could maximize the propagation of their genes by producing sons, Hölldobler and Wilson argue, instead of helping their mother produce brothers. Workers would benefit from producing sons rather than helping the queen produce brothers, Hölldobler and Wilson explain, because a worker would likely share half of her genes with a son, but only one quarter of her genes with a brother. Hölldobler and Wilson conclude that the observed behavior of queens supports parental manipulation over kin selection theory because the queen seems to be maximizing her own reproductive success at the cost of the workers' reproductive success.

Hölldobler and Wilson finish the ”Testing the Kin Selection Theory” section of ”Altruism and the Origin of the Worker Caste” by examining the sex ratio of reproductively active ants produced by various kinds of ant colonies. A sex ratio describes the number of females in a group of organisms relative to the number of males. If a group of ants had a 4:1 sex ratio in favor of females, there would be four female ants for every one male ant in the group. Hölldobler and Wilson list the sex ratios of reproductively active ants that kin selection theory predicts for colonies with different numbers of queens. Next, Hölldobler and Wilson compare the predicted sex ratios with observational data on the actual sex ratios of reproductively active ants produced by those three kinds of ant colony. After comparing the observed sex ratios of reproductive ants from different types of colonies with the sex ratios predicted by kin selection theory, Hölldobler and Wilson conclude that observational data generally supports kin selection theory.

In the next section, ”Eusociality and Chromosome Numbers,” Hölldobler and Wilson briefly explore the role of a species' chromosome number on the development and maintenance of eusocial traits. Hölldobler and Wilson begin ”Eusociality and Chromosome Numbers” by stating that colonies of social insects are more harmonious when the colony members are more closely related. Thus, Hölldobler and Wilson reason, mechanisms that increase genetic similarity within social insect colonies should propagate in populations of eusocial insect species. It is possible, Hölldobler and Wilson claim, that eusocial insects evolved a greater number of chromosomes as a means of reducing the genetic variance within a colony.

Hölldobler and Wilson explain that a higher number of chromosomes increases genetic similarity between parents and offspring because larger numbers of chromosomes tend to cause parental genetic material to pass onto offspring in smaller rather than larger packets. The more a parent's genetic material gets broken up, the more component parts there are to potentially transfer to the child. The more component parts there are to transfer, the greater the number of possible genetic combinations a child can receive from her parent. Hölldobler and Wilson claim that a greater number of potentially inheritable genetic combinations causes the parent's genetic material to be more evenly distributed across her offspring. As a result, the offspring will tend to more genetically similar to each other than they would have been had their parents' genetic material been transferred to them in large chunks.

At the end of ”Eusociality and Chromosome Numbers” Hölldobler and Wilson consider whether data on the chromosome numbers of social insects supports the hypothesis that a higher number of chromosomes led to the development of eusocial traits in social insects. According to Hölldobler and Wilson, research confirms that eusocial insect species such as ants and termites have more chromosomes than the non-social species of insects most closely related to them. Though a high chromosome number seems to be associated with eusociality, and therefore with the development of the worker caste in ants, Hölldobler and Wilson conclude that there is not yet enough information to determine whether a higher number of chromosomes is a cause or effect of eusociality.

In the final section of ”Altruism and the Origin of the Worker Caste,” titled ”Overview,” Hölldobler and Wilson summarize the theoretical trends that have dominated research on the origin of the worker caste during the last half of the twentieth century. In the 1960s and early 1970s, Hölldobler and Wilson claim that researchers favored kin selection theory as an explanation for the origin of the worker caste. Then, during the latter half of the 1970s, Hölldobler and Wilson write that parental manipulation theory gained popularity among researchers at the expense of kin selection theory. Finally, in the 1980s, Hölldobler and Wilson claim that kin selection theory regained popularity as researchers began to appreciate the ways in which parental manipulation theory and kin selection theory complement each other.

Hölldobler and Wilson conclude the ”Overview” section by suggesting directions for future research on the origin of the worker caste. Hölldobler and Wilson state that ants may have become eusocial as early as the late Cretaceous Period, and that there were no described species of ants in the early stages of eusociality. Hölldobler and Wilson suggest that bees and wasps are the best social insects for studying the origin of the worker caste because there are living species of bees and wasps ranging from solitary social practices to eusocial behaviors.

The Ants received generally positive reviews, winning the Pulitzer Prize for general non-fiction in 1991. Modern Library, a US publishing company, ranked The Ants number twenty-seven on its list of ”100 Best Nonfiction Books Written in English during the 20th Century.” Reviews of The Ants appearing in the Washington Post, Time Magazine, Scientific American, The New York Times, and Nature, praised Hölldobler and Wilson for writing The Ants in a style that balances accessibility with clarity.

After tentatively endorsing kin selection theory as an explanation for the origin of the worker caste in ”Altruism and the Origin of the Worker Caste,” Hölldobler and Wilson published work jointly and separately arguing that kin selection is a negligible force in the evolution of eusociality. According to the later work of Hölldobler and Wilson, kin selection theory is too narrow to explain the transition from solitary organisms to eusociality. Hölldobler and Wilson argue in their later work that group selection is the primary force in the evolution of eusociality. By group selection, Hölldobler and Wilson mean a process in which groups of individuals interact with other groups of individuals and their environment in such a way that the genes of individuals are selected to promote the survival and reproduction of the group.

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