

Christian Peeters and Bert Hölldobler's Experiments on Reproduction in Indian Jumping Ants (1991–1994)

Between 1991 and 1994, Christian Peeters and Bert Hölldobler studied the reproductive behaviors of the Indian jumping ant (*Harpegnathos saltator*), a species native to southern India. They conducted experiments as part of a larger investigation into conflict and reproductive behavior among ants. Peeters and Hölldobler discovered that Indian jumping ant colonies contained both sexually reproductive workers and egg-laying queens. In most other species of ant, the queens are the only sexually reproductive individuals. After conducting their experiments, Peeters and Hölldobler argued that queens and sexually reproductive workers cooperated in the Indian jumping ant species to establish and preserve new colonies.

Peeters and Hölldobler began working together at the University of Würzburg in Würzburg, Germany. Peeters studied zoology at the University of Witwatersrand in Johannesburg, South Africa, and joined Hölldobler's ant research team at the University of Würzburg as a post-doctoral fellow in 1991. Hölldobler won the Gottfried-Wilhelm-Leibniz Prize in 1990, a large research grant from the German Science Foundation, and he used the money to hire early career researchers like Peeters. Peeters and Hölldobler began collaborating on a series of academic articles about conflict within ant colonies.

Peeters and Hölldobler investigated the behaviors of the two types of ant that make up an ant colony, worker ants and queen ants. Queen ants are physically specialized to reproduce, and though multiple egg-laying queens sometimes coexist in a single colony, researchers at the time stated that most ant species lived in single queen colonies. Queen ants lay eggs that can develop into worker ants, male ants, or queen ants. Worker ants almost never reproduce, and are always female. Male ants and queen ants, the two types of ant physically specialized for reproduction, only develop once a year just before mating season. Male ants inseminate virgin queens during mating season and die shortly after. The newly inseminated queens then go on to found new ant colonies by laying eggs that develop into workers.

Peeters and Hölldobler studied how queen ants inhibited workers from laying eggs. As Hölldobler explained in his 1990 book *The Ants*, queens prevent workers from laying eggs in multiple ways. The queens of many ant species exude a chemical that inhibits workers from producing eggs, and the queens of some ant species physically attack fertile workers.

As part of their investigation into the reproductive behaviors of workers and queens, Peeters and Hölldobler began studying ants in the Ponerinae subfamily. Ants in the Ponerinae subfamily are different from other subfamilies of ant because Ponerine ants are phylogenetically primitive, meaning they have more characteristics in common with their hypothesized wasp ancestors than other living subfamilies of ant. Though the workers of most ant species lack the sexual organs needed to mate with males and produce eggs, Peeters noted that the workers of some Ponerine species retained those sexual organs. Peeters also noted that queen ants in the Ponerinae subfamily tended to produce fewer eggs than the queens of other subfamilies. As a result, Ponerine colonies tend to be small relative to the colonies of other subfamilies. One of the Ponerine species studied by Peeters and Hölldobler had an average colony size of fifty-four ants, for instance. The relatively small size of Ponerine ant colonies paired with the fertility of Ponerine enabled Peeters and Hölldobler to more easily study ant reproductive behaviors.

During the early 1990s, Peeters and Hölldobler performed experimental work on a Ponerine ant species often called the Indian jumping ant. Peeters and Hölldobler excavated forty-four Indian

jumping ant colonies in Karnataka, India, between 1991 and 1994. Peeters and Hölldobler counted the number of workers and queens in each colony. To determine the number of inseminated, egg-laying workers, Peeters and Hölldobler dissected the sexual organs of 865 workers sampled from fifteen of the forty-four excavated colonies. Peeters and Hölldobler determined whether or not a worker had been inseminated by testing the worker's sexual organs for sperm. They determined whether or not a worker had been laying eggs by checking the worker's sexual organs for yellow bodies. Yellow bodies are accumulations of a specific kind of cell that eggs deposit as they leave the body of an egg-laying ant. The more yellow bodies Peeters and Hölldobler found inside a worker, the more eggs that worker had been laying.

Having compiled their data, Peeters and Hölldobler found that inseminated workers were common among Indian jumping ants. Of the fifteen colonies Peeters and Hölldobler sampled, fourteen of those colonies contained at least one inseminated worker. Seven of those fifteen colonies had no queens, making workers the only egg-layers in those colonies. Six of the fifteen colonies contained a queen who was the sole egg-layer of the colony. Of those six colonies in which queens were the only egg-layers, five contained inseminated workers that had not laid any eggs. Finally, in two of the fifteen colonies sampled, Peeters and Hölldobler found egg-laying workers living alongside an egg-laying queen.

From that data, Peeters and Hölldobler inferred some of the reproductive practices of queens and workers. Because Peeters and Hölldobler found inseminated workers living alongside queens, they concluded that workers were mating with males while the queens were alive. The researchers argued that inseminated workers laid no eggs in most of the colonies that still contained a queen, because the queens inhibited the workers' ovaries from producing eggs. In those two colonies for which Peeters and Hölldobler found workers laying eggs despite the presence of a queen, Peeters and Hölldobler discovered that the egg-laying workers had a small amount of light colored yellow bodies in their sexual organs, meaning the workers had only recently begun laying eggs. Peeters and Hölldobler interpreted that result as evidence for the claim that Indian jumping ant workers slowly begin laying eggs as the queen nears the end of her life and becomes a less productive egg-layer.

To explain the reproductive practices of Indian jumping ants, Peeters and Hölldobler articulated a new hypothesis for the lifecycle of Indian jumping ant colonies. An Indian jumping ant colony, Peeters and Hölldobler argued, begins with a single inseminated queen founding a colony. Only queen Indian jumping ants can start new colonies. The queen then produces workers to populate the new colony while producing males and virgin queens once a year in preparation for mating season. During mating season, the males and virgin queens leave the nest to mate with the males and virgin queens of other colonies. However, instead of mating exclusively with virgin queens, some males mate with workers from other colonies. Those inseminated workers do not lay eggs until their queen dies or nears the end of her life. Once the queen dies, the inseminated workers begin laying enough eggs to sustain the colony and to produce males and virgin queens during mating season. According to Peeters and Hölldobler, when an Indian jumping ant colony contains only workers, it is in the final stage of its lifecycle.

Finally, Peeters and Hölldobler provided a hypothesis for why the reproductive practices of Indian jumping ants differ from the reproductive practices of other ant species in which workers never reproduce. According to Peeters and Hölldobler, Indian jumping ant queens do not fully inhibit workers from reproducing because Indian jumping ants have evolved a set of behaviors that enables a colony to transition from one egg-laying queen to multiple egg-laying workers. Peeters and Hölldobler argued that Indian jumping ants have evolved that set of behaviors because the nests Indian jumping ants build require too much work from the ants to build them for those ants to abandon them every time a queen dies. Unlike other Ponerine ant species, Indian jumping ants construct elaborate underground nests to survive in the flood prone plains of southern India. Peeters and Hölldobler concluded that Indian jumping ants evolved an unusual set of reproductive behaviors to get more use out of the significant labor investment that their nests represent.

Peeters and Hölldobler published the results of their research in a 1995 article titled "Reproductive Cooperation between Queens and Their Mated Workers: The Complex Life History of an Ant with a Valuable Nest." Researchers generally accepted Peeters and Hölldoblers' explanation of the

Indian jumping ant's reproductive cycle. Academic articles attempting to synthesize data about the reproductive practices of ants have cited Peeters and Hölldobler's article as documenting a rare reproductive scheme in ants. Other ant researchers, and Peeters and Hölldobler, continued to study the reproductive practices of Indian jumping ants by designing experiments to uncover the role of chemical communication in Indian jumping ant reproductive practices.

Sources

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