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# Were Workers of Eusocial Hymenoptera Initially Altruistic or Oppressed?*

**(bee/*Lasioglossum zephyrum*/queen/social behavior)**

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**ABSTRACT** **Studies of a primitively eusocial halictid bee, *Lasioglossum zephyrum*, strongly suggest that a major factor in originating a worker caste is selection at the individual level for queens that control associated adult females. Even in this scarcely social form, the queen inhibits other adult females from becoming queens, perhaps by her high level of activity and frequent nudging in the nest. Queens are behaviorally less varied than workers and show specialization, particularly in frequency of nudging (which is concentrated on the worker with largest ovaries) and of backing. Backing draws workers, especially those with slender ovaries, down to lower parts of the burrows where the stimuli for cell construction and provisioning probably operate. Eating of worker-laid eggs by queens was also noted. In spite of the suggestion that queens have evolved to control their workers rather than that workers have evolved to help their queens, both may well have occurred, for these processes are not mutually exclusive; moreover, social attributes mutually beneficial to both castes no doubt have arisen.**

Most writers on castes in eusocial Hymenoptera stress one or another principal explanation for the origin and evolution of a worker caste, i.e., a class of individuals of reduced productivity. The principal theories are as follows:

(*a*) The worker caste has arisen by kin selection such that the reduced reproductivity of a worker is more than compensated in terms of fitness by the increased reproductivity of the associated queen. The worker, which has given up part of its reproductivity, and is therefore altruistic in the sense of Hamilton (1), helps its mother, the queen, produce more offspring, which are brothers and sisters of the worker. If the queen mates only once, sisters in haplodiploid insects like Hymenoptera are more closely related to one another than a mother is to her daughter. Therefore, more genes like those of the worker may be contributed to the next generation by an individual that joins her mother as a worker and helps to produce siblings than by one that leaves her mother, mates, and produces an equal number of offspring. Hamilton, in a series of important papers (1–3), has explained this concept in detail.

(*b*) The worker caste has arisen by individual selection on mothers resulting in their control of the activities of their female offspring. The influence that even a solitary mother hymenopteron exercises on her immature progeny by feeding and protecting them continues, in eusocial species, past maturation of the daughters. The queen is somehow able to keep them in the nest and diminish their reproductivity, and in a sense is parasitic upon her daughters. Altruism is not necessary to explain such developments although it will result from them; selection at the individual level operating with respect to queens, favoring those best able to keep and control workers, and thus enhancing their own productivity of sexual forms, is an adequate explanation. This concept, implied by various earlier authors, is discussed in greater detail and advocated by Alexander (4).

(*c*) The worker caste has arisen by selection such that individuals evolve different social attributes that are mutually beneficial. The benefits may be simultaneous, resulting from mutualistic social attributes (5), or sequential as in reciprocal altruism (6). Selection at the individual level could function with respect to the socially important characteristics of queens, as well as for those of workers to the extent that the workers reproduce. Common characteristics like mutual tolerance would be especially easily explained in this way but other kinds of attributes may also be mutually beneficial. If disadvantaged (e.g., by season of production) females remain with their mother and are more productive than if they tried to establish their own nests, they could benefit both themselves and their mother, producing a primitively eusocial colony of a "queen" and "workers" that lay eggs; no altruism is involved.

The three theories summarized above are not mutually exclusive. Each may contribute a share to many of the episodes of social evolution in Hymenoptera. Since 1964 (1, 2), however, almost all authors have emphasized the idea of kin selection favoring altruistic social behavior (theory *a*). Nevertheless, alternatives have been emphasized by Michener (7), Lin and Michener (5), and most recently by Alexander (4). The present paper provides additional support for the theory of control by the queen (theory *b*).

Hamilton's papers examine the problem of social evolution in insects almost entirely from the workers' viewpoint. This emphasis is understandable since the origin and evolution of castes of reduced reproductivity has been a problem for evolutionists ever since Darwin. Evolution of worker attributes, according to Hamilton's views, results from the ability of workers to promote production of genes like their own. Social attributes of the queen, however, must also be considered. Such features can result from individual selection acting on queens. Evolution of worker attributes that permit control by the queen may also be important. Such worker attributes could be favored by selection for queens that produce controllable workers.

We have studied *Lasioglossum zephyrum*, a small eusocial halictid bee that burrows into earthen banks. It falls in a subgenus (*Dialictus*) containing solitary as well as social

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species, and in a genus with subgenera that are wholly solitary (e.g., *Lasioglossum* s. str.). Thus it is closely related to solitary species. The social level of *L. zephyrum* is about as low as that of any known eusocial insect. This statement is based on a number of attributes relating to the degree of difference between the worker and queen castes and on the assumption that minimal differences are associated with early stages in the evolution of caste differences. Workers and queens in *L. zephyrum* are indistinguishable externally, although there is a minor average size difference. The queen was initially defined as the bee with the largest ovaries but there is a continuum in ovarian size from workers with scarcely enlarged ovaries to queens, and intermediates are common (8, 9). As indicated below, queens are more distinct behaviorally. Nests containing only one female are not uncommon and mean colony size, even in late summer when nests contain nonworking young females that will overwinter, is only 14 bees (8). Queens are relatively short lived although they live longer than workers; bees that overwinter and become queens die and are replaced by mid-summer. Caste determination does not occur until the adult stage; all or most young adult females are gynes and have the potentiality to become either queens or workers. Males are produced throughout the reproductive season (8–10). (As in other eusocial Hymenoptera, males play no role in the colonial life; all bees mentioned in the following paragraphs are females.)

Since the castes cannot be distinguished on sight, a behavioral study to ascertain functional differences between castes, i.e., division of labor, presented certain problems. Colonies were maintained in earth between sheets of glass (11). They consisted either of an overwintered queen and her female progeny or were made up artificially by placing field-collected spring or summer pupae in the nests (9). Bees were marked for individual recognition with quick drying "Dope" paint. Thirty-seven colonies were studied, ranging in size from 2 to 6 females. Activities in the nests were recorded for a total of 219 hr; the results have been analyzed in detail by Brothers and Michener (12).

*Queen Replacement.* From 12 colonies the queen, recognized behaviorally (see below) and sometimes verified later by examination of the ovaries, was removed. In all but one case another bee soon took up queenlike behavior, in at least one instance within 4 hr. Dissections a few days later showed that the replacements had enlarged ovaries and must have become functional queens. From four nests, replacement queens were themselves removed; when a second replacement was clearly recognizable it was removed, the process continuing until the resulting colony contained only two bees—the last replacement queen and one worker (12).

These observations suggest that the queen in some way inhibits ovarian development and queenly behavior in nestmates. This is control by the queen.

*Behavioral Categories.* For each of 10 behavioral categories listed below, the bees of each colony were placed in rank order, 1 for minimal activity, 2, 3, 4, 5, or 6 for maximal activity depending on colony size. Trends within each behavioral category were investigated by plotting the proportion of the total of that activity in the colony contributed by each bee against the rank of the bee for that activity. The mean proportion of each rank was then plotted (and connected by lines) for colonies of two, three, four, five, and six bees (12).

For nearly all categories queens are concentrated in one or the other extreme rank rather than in intermediate ranks. In the following list, the rank in which queens are concentrated (maximum, minimum, intermediate) is indicated for each category, together with the probability of random distribution of queens over the ranks for that category:

1a. Nudging: max.; $P \ll 0.01$, $n = 25$ colonies.
1b. Being nudged: min.; $P \ll 0.01$, $n = 25$ colonies.
2a. Backing: invariably max.; $n = 12$ colonies with complete ovarian data.
2b. Following: min.; $P \ll 0.01$, $n = 25$ colonies.
3a. Passing: min.; $P \ll 0.01$, $n = 25$ colonies.
3b. Being passed: int.; $0.9 > P > 0.5$, $n = 25$ colonies.
4. Guarding: min.; $P \ll 0.01$, $n = 25$ colonies.
5. Pollen collecting: min.; $0.05 > P > 0.01$, $n = 9$ colonies.
6. Working on burrows: max.; $0.1 > P > 0.05$, $n = 23$ colonies.
7. Working on cells: int.; $0.05 > P > 0.01$, $n = 17$ colonies.

[For each test of probability, the distribution was divided into three groups—bees showing maximal behavior (maximum rank), those showing minimal behavior (rank 1), and intermediates—except that for pollen collecting the distribution was divided into two equal groups. Colonies of two bees were excluded for these chi-square tests.]

For several categories the lines connecting means are concave as a result of the disproportionately greater contributions to the behavior by the higher ranking members; the concavity indicates behavioral specialization. The frequency of individual colonies showing concave curves over the last three ranks was significantly different from that showing nonconcave curves for nudging ($0.05 > P > 0.01$; $n = 24$) and backing ($P \ll 0.01$; $n = 25$) but not for the other attributes. Nudging and backing are therefore the most distinctive behavioral attributes of queens.

Of course certain types of workers also appear in maximum or minimum numbers in certain ranks. Only for pollen collecting are the curves that connect the rank means conspicuously concave in such a way as to suggest specialization of certain workers for this activity ($n$ too small to demonstrate significance). For some colony sizes they are concave also for guarding, but the frequency of colonies with concave curves for this behavioral category was not significantly different from that with nonconcave curves ($P > 0.05$; $n = 25$). For most behavioral categories no particular workers show such signs of specialization.

If worker altruism is of prime importance, the worker caste might reasonably show greater deviation from the solitary type than do queens in characteristics related to social interactions; queens should be more modified if control by them is of greatest significance; both castes should show considerable modification if mutualism or both altruism and control are of major importance. The extreme positions (maximal or minimal ranks) of the queens for so many behavioral categories (of which 1 to 4 in the above list are not developed in solitary bees) suggest that queens are behaviorally more specialized than workers, taken as a group. Because of the generally reciprocal relationships between certain behavioral categories, e.g., backing and following, the maximal positions of queens for nudging and backing essentially insure their minimal positions for being nudged, following, and passing, and probably explain their rank for guarding. The apparent specialization of workers for pollen collecting is largely a result of reduction of this activity by the queen. This specialization of the queen is likely to have resulted from her acquisition, along with the onset of eusocial behavior, of the ability to control workers. If the major factor leading to the appearance of a worker caste had been altruism, one ought to find evidence of it, other than the reduced ovarian size and reduced frequency of mating which could both result from queen control.

*Nudging and Backing.* Further evidence of the specialization of the queen and of her potentiality for controlling workers appears when her behavior is examined in greater detail. The queen is conspicuously the most active bee in the colony. Her specialized high rank positions for nudging and backing are indicative of great activity, although much of her moving about does not culminate in either of these analyzed behavioral categories.

Nudging occurs when a bee in a burrow approaches another, hesitates, and then moves forward in a short, sharp movement that brings her face in contact with the other bee. The mandibles are not open as in overtly aggressive activity but we suspect that this is ritualized agonistic behavior derived from that which occurs, with open mandibles and sometimes with stinging, in groups of female solitary bees (conceivably leading to their subsequent solitariness), or in dominance-subordinance interactions in colonies of bumblebees (13) or wasps (14, 15).

Any bee may nudge and any bee may be nudged, but queens are responsible for much of the nudging in any nest. The most nudged bee is usually in that position because of more frequent nudging by the queen than by other bees. Among workers there is a positive relationship between frequency of being nudged and ovarian size. Therefore, it appears that queens concentrate their nudging on workers with enlarged ovaries. Such workers are commonly guards and are usually at or near nest entrances.

Nudging by the queens is commonest in the upper parts of the burrows. When a queen nudges a guard, it usually does not turn or follow her. The disturbance, however, may be important in inhibiting further ovarian development by the worker (guard). When a queen is removed from a colony with four or more bees, it is usually a worker that we believe from behavioral data to have intermediate-sized ovaries (for workers) and that is neither a guard nor a forager, that becomes the replacement queen. The mean rank of replacement queens for being nudged, before removal of original queens, was about the second to highest rank ($n = 11$). It seems likely that the worker with the largest ovaries is so traumatized by the queen that it is unable to react promptly to the disappearance of the queen. The results would be the same if the control were exercised chemically, for example by a hypothesized substance that allows bees to respond to other individuals as though they knew the size of their ovaries (see discussion by Brothers and Michener, 12).

A preliminary experiment in which we artificially disturbed newly emerged adult bees may be looked at either as suggesting that nudging can inhibit ovarian enlargement or simply as evidence that disturbance by us can have that effect. Clearly, it is only suggestive, so far as nudging is concerned. Fifteen colonies were established with four young bees each. (One or more bees in several colonies died, escaped, or were parasitized by a strepsipteron, *Halictoxenos*.) The nests were closed with plastic containers provided with honey and *Typha* pollen, as described by Kamm (16). In five nests a small iron bead was moved around in the burrows by means of a magnet outside the nest. This was done six times per 24 hr, for 5 min each time, for a week. The objective was to simulate nudging, but jumpy movement of the bead made convincing simulation difficult. A second set of five similar nests was subjected only to moving the magnet over the nests, without iron beads inside. The third or control group of five nests was undisturbed. In the first group, no cells were made; most of the bees burrowed through the soil and no ovarian enlargement occurred. (Two colonies were destroyed by Strepsiptera.) In the second group a few cells, at least one per nest, were made; none was provisioned, several bees showed various degrees of ovarian enlargement (one to a greater extent in each nest) but few had an egg ready to be laid when dissected at the end of the week. In the control group one colony was destroyed by Strepsiptera but each of the others had made and provisioned cells and laid eggs; one bee in each was recognizable as a queen upon ovarian examination.

Nudging is closely related to backing. When a bee nudges another that is not a guard from behind, the latter commonly turns around to face the nudger. The nudger may now back rapidly down the burrow, and if followed by the nudged bee, will continue backing for several centimeters. Backing may also occur without nudging or turning after two bees have approached one another; instead of passing, the lower bee may back. Backing is not continued if following does not occur; we did not categorize backing as such unless it continued for over one centimeter and when this was the case, following consistently accompanied it. As indicated above, the queen was in the highest rank for backing in every colony.

Backing appears to draw workers, other than the guard, down into the nest, to the area where cells are being made and provisioned. It seems likely that by getting workers into the part of the nest where the stimuli for cell constructing, provisioning, and the like are present, the queen increases the probability that the workers will respond to those stimuli. It is workers with slender ovaries, those that follow most readily, that usually fall in the highest rank for working on cells and for foraging to provision completed cells. Again this looks like control of workers by the queen rather than simply altruism by workers.

*Multivariate Analysis.* Using all the behavioral categories listed above except pollen collecting, a principal components analysis and stepwise discriminant (canonical) analyses (using proportions of total activity of each bee in its nest as well as using rank positions) were made. In each analysis queens formed a cluster disjunct from a rather scattered group of workers. This finding supports the concept of the queens as the behaviorally less variable and therefore probably more specialized caste in *Lasioglossum zephyrum*.

*Oophagy.* Also suggestive of control by the queen is our scant data on oophagy. In all three instances in which an egg was eaten and in which the identity of the bees involved was known, a queen ate an egg laid by a worker and replaced it with one of her own.

**Discussion and conclusions**

We have cited findings on queen replacement and behavioral attributes of queens and of workers that suggest that queens have evolved to control their workers even in this very primitively social bee rather than that workers have evolved as altruists to help their queens. Both processes may well have contributed to the evolution of eusocial behavior in *L. zephyrum;* indeed worker altruism must be present unless the relationship is predominantly mutualistic but we think that control by queens has been the principal factor.

The question then arises as to why a worker would not simply fly away and thus escape parental influences. Maternal control may reduce the likelihood that a young female will abandon her mother. For example, constant drawing of bees with slender ovaries down into the nest by the queen may keep them there during much of their early adult lives. This may reduce their probability of mating. The same behavior may reduce their opportunities to eat in the field, thus tending to keep the ovaries slender. Data on the ontogeny of worker behavior would aid in recognizing such maternal control.

Another possible explanation for the failure of young bees to leave their mothers involves mutual benefits to both queen and workers. Given (*a*) the difficulties and dangers of establishing a new nest, (*b*) the low survivorship of nests occupied by lone bees (there is no guard) (8), (*c*) the reproductive activities that some workers have even in the presence of queens and the workers' possible importance as male-producers (5), and (*d*) the possibility that the queen will die so that a worker can replace her, selection at the individual level may favor staying in the maternal nest even though this means becoming a worker. Because of the influences of temperature, day length, and colony size on cell size and amount of provisions, bees produced in summer average smaller than those produced in autumn (16). Smaller females probably have a lower reproductive potential than larger ones and thus are reproductively disadvantaged—in the terminology of Lin and Michener (5), they are environmentally disfavored females. Such bees would be particularly subject to selection at the individual level for staying in the maternal nest. This is a situation similar to that described by West (17) except that in her case the workers were nonreproductive and therefore must have been altruistic rather than mutualistic.

In answer to the query in the title, the evidence indicates control by the queen ("oppression") as the primary favor leading to the appearance of a worker caste. Worker altruism is a necessary consequence of eusocial systems unless, with somewhat reproductive workers, the system is mutualistic; altruistic behavior should thus be evident even if there were no control by queens. By contrast, control by queens is not in theory a necessary aspect of eusocial behavior, since workers could presumably coordinate their activities with those of the queen without being controlled by her. The occurrence of control by queens in all eusocial groups, here described even in one of the most primitively eusocial forms, suggests that such control has fundamental importance.

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