Insectes Sociaux, Paris
1982, Volume 29, n° 2, pp. 125-137

QUEEN-WORKER BEHAVIOR AND NESMATE INTERACTIONS IN YOUNG COLONIES OF *LASIOGLOSSUM ZEPHYRUM*

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Reçu le 3 août 1980. Accepté le 17 octobre 1980.

SUMMARY

Nestmate interactions and caste differences in behavior were studied in young, artificial colonies of *Lasioglossum zephyrum.* Workers avoided or withdrew from interactions with queens more often than from interactions with other workers. Queens sat in locations where they can potentially influence the behavior of nestmates more frequently than did workers. Queens also made more brief visits to cells than did workers.

It is hypothesized that workers avoid the queen in order to reduce the frequency of being nudged by her. The queen's tendency to sit in locations where the potential for influencing nestmate behavior is high may be a manifestation of her role as a coordinator of worker activities. Frequent but brief visits to cells may provide the queen with up-to-date information on the statuts of each. Later, she may use this information to modify her influence on worker behavior.

RESUME

Le comportement des reines et des ouvrières et leurs interactions dans des jeunes colonies de Lasioglossum zephyrum

Les interactions entre individus du même nid et les différences de comportement entre les castes ont été étudiées dans de jeunes colonies artificielles de *Lasioglossum zephyrum.* Les ouvrières évitent ou quittent les contacts avec les reines plus souvent qu'elles n'évitent les contacts avec d'autres ouvrières. Les reines se tiennent en des lieux où elles peuvent influencer le comportement des autres individus du nid plus fréquemment que ne le font les ouvrières. En outre, les reines font plus souvent des visites brèves aux cellules que les ouvrières.

Ces comportements peuvent suggérer que les ouvrières évitent la reine pour réduire la fréquence des contacts avec elle. La forte tendance de la reine de se placer à des endroits où elle peut fortement influencer le comportement des individus du même nid peut être une manifestation de son rôle de coordination des activités des ouvrières. Les visites aux cellules, fréquentes mais brèves, peuvent renseigner la reine sur l'état actuel de chaque cellule. Par suite, il est possible qu'elle utilise ces informations pour modifier le comportement des ouvrières.

INTRODUCTION

The primitively eusocial organization of the halictid, *Lasioglossum zephyrum,* has received much attention in recent years. Behavioral and morphological differences between queens and workers have been described by BATRA (1966), MICHENER, BROTHERS, and KAMM (1971), MICHENER and BROTHERS (1974), and BROTHERS and MICHENER (1974). These studies indicate that the queen (the individual with the largest ovaries) nudges more than other bees do in interactions with nestmates and is nudged the least. Episodes of backing-following, in which one bee backs away from another and the second follows, generally involve the queen as the backer and a worker as the follower.

MICHENER and BROTHERS (1974) hypothesized that nudging may inhibit ovarian development in workers and that backing-following may function to draw workers down into the nest where stimuli for cell construction and provisioning are present. More recently, BREED and GAMBOA (1977) concluded that the queen plays a greater role than was originally thought in stimulating and coordinating the activities of workers. Queens were observed to lead returning foragers to the cell being provisioned or to station themselves below the cell entrance prior to the arrival of the pollen-carrying bee. Workers became disoriented when the queen was either taken out or diverted to some other task.

This paper provides new information on queen-worker differences and nestmate interactions in newly established colonies of *L. zephyrum.* Further aspects of the queen's behavior that enable her to coordinate the activities of workers are discussed, as are data bearing on the dominant-subordinate relationship of queens and workers. Observations were made of young colonies (1-17 days of age) so that the events leading to the emergence of the queen and worker castes in groups of undifferentiated adult females could also be followed. The results presented in this paper concern behaviors which do not show any significant changes over time once a queen has been determined. Included are many behaviors that have not been considered previously as well as some that have been. A subsequent paper will focus on (a) changing behavior patterns in young colonies and (b) the differentiation of the queen and worker castes.

MATERIALS AND METHODS

Establishment of colonies

Seventeen colonies of bees, all from Douglas County, Kansas, were set up in artificial nests similar to those described by Michener and Brothers (1971), except that the nests were closed systems, connected by short (6-8 cm) plastic tubes to plastic vials that contained honey water and *Typha* pollen (Kamm, 1974).

Colonies 1-14 were composed of groups of sisters reared in the laboratory. To form each colony, individuals were removed from their cells in a source nest as they became adult females ; they thus had no contact with the adult members of the parental colony. They were marked with enamel for individual recognition. Colonies 1-6 and 11-14 eventually contained six bees ; colonies 7 and 8 contained five and colonies 9 and 10, four.

Colonies 15-17 were set up in a similar manner, but were not composed of sisters. These colonies were started with callows that had been collected in the field as pupæ. No two bees in a given colony were taken from the same nest in the field. Colony 15 contained six bees, colony 16 five and colony 17 three.

Behavioral observations

All nests containing two or more bees were watched for 25 to over 300 minutes daily for six to seventeen days, except that for a few nests, observations were occasionally made every other day, and in a few instances, three or more days separated one session from the next. The 17 colonies were observed for a total of 16,821 minutes (mean : 958 min., range : 452 to 1544 minutes). Descriptions of the various classes of behavior that were recorded follow :

A *nudge* was recorded whenever one bee touched another with its head or antennæ but did not immediately proceed to pass the contacted bee. This is a more inclusive definition than that of Brothers and Michener (1974). As defined by those authors, a nudge occurred only when one bee approached another, hesitated, then contacted the other bee in a short, sharp movement.

An *approach* was recorded for nests 10-17 if the head of a moving bee came within one centimeter of the head of a stationary nestmate, provided that the immediately preceding behavior exhibited by either bee was not actually or potentially directed at the other. A record was also kept of *double approaches*, i.e., instances in which two bees moving in opposite directions approached to within approximately one centimeter of each other.

A stationary bee approached from the front by a nestmate may back away before the approaching bee contacts it. This is defined as *backing*. *Retreating* consists of two classes of behavior : those that involve forward movement after being contacted on the abdomen and those that involve backward movement after being contacted on the head. Finally, a bee that is facing another bee may lead that individual along the tunnel, either towards or away from the nest entrance. Interactions of this sort are defined as *backing-following* if the distance covered by the two bees is greater than one centimeter. Backing-following may be initiated by a nudge or by the approach of a nestmate. Thus, backing, and backing in the context of backing-following, are not identical terms.

One purpose of the study was to record the sequence of behaviors exhibited during interactions between bees. The principal types of interactions followed were those initiated by approaches and those initiated by nudges.

A stationary bee approached by a nestmate typically exhibited one of five responses : it either (1) backed, (2) nudged the approaching bee, (3) *lunged* (moved forward and back in one quick motion without contacting the approaching bee), (4) *advanced* (moved forward, followed usually by a pass), or (5) exhibited *no response*, that is, remained in the same position. In a few cases, *C postures* were seen (aggressive responses described in BELL and HAWKINS, 1974).

The subsequent behavior of the approaching bee was categorized as follows: (1) *sat/groomed* (the bee stopped and either remained temporarily motionless or groomed), (2) *passed,* (3) followed, (4) *executed a turn around* (the bee stopped and turned around so that it was facing in the direction from which it came), (5) nudged, (6) lunged, and (7) *other* (the bee went into a nearby cell, down an adjacent side tunnel, etc.).

Bees that approached one another either (1) moved backwards, (2) nudged, (3) lunged, (4) passed, (5) followed, (6) executed a turn around, (7) sat/groomed, or (8) engaged in other behavior.

The responses of a bee nudged on the head were recorded as follows: (1) retreated, (2) executed a turn around, (3) nudged, (4) lunged, (5) *maintained position* (lumped into this category were sitting, grooming, and pressing dirt against the side of a tunnel or cell but not moving towards or away from the nudger), (6) advanced, (7) followed, and (8) other. The different responses of a bee nudged on the abdomen were scored as follows: (1) retreated, (2) executed a turn around, (3) *executed a double turn around* (the bee turned around, then turned around again so that it was facing in the original direction), (4) maintained position, and (5) other.

A bee that is guarding sits at the nest entrance facing outward. In our artificial nests, the position generally occupied by the guard was at the outer end of the plastic tube that opened into the vial containing honey water and pollen, though disturbances sometimes caused the guard to move 2-3 centimeters backwards. Quite frequently other bees lined up behind the guard, forming a queue of as many as six bees. The individuals in these queues were separated by distances ranging from negligible to several centimeters. Much coming and going as well as switching of positions resulted in frequent changes in the number and sequence of bees in a queue.

Preliminary observations indicated that the position at the junction of the plastic entrance tube and the soil substrate was often occupied by a sitting bee. Some queues extended this deep into the nest. When only a few bees were behind the guard, the innermost would sometimes nonetheless be at this junction, 5-7 centimeters behind the bee in front of it. Positions farther back in the main tunnel, but still toward the entrance of the nest, were much less frequently occupied and bees in such positions were not considered part of the queue. These findings provided the basis for the following definitions:

Guarding: sitting within three centimeters of the nest entrance with no other bees closer to the nest opening.

Sitting (alone or in a queue) near the nest entrance: sitting farther than three centimeters from the nest entrance but no deeper than the soil-tube junction, or sitting within three centimeters of the nest entrance but behind one or more bees.

The amount of time in each observation period that queens and workers engaged in these behaviors was recorded. When queues were present in the entrance tube, data were also collected on the amount of time bees spent sitting in particular positions (i.e., guard, second bee, third bee, etc.).

For nests 10-17 a record was kept of time spent *sitting elsewhere in the nest* (defined as sitting in any section of the burrows, but not in cells). Durations were not recorded since it was not possible to accurately keep track of guarding, sitting near the nest entrance, and sitting elsewhere. Instead, a bee was scored as sitting in a particular location in a burrow if it remained virtually motionless for an entire minute; the bee could shift its posture slightly, but it could not groom.

For nests 1-9 data were gathered on *visits to cells.* Episodes in which a bee inserted its head into a cell but did not completely enter were recorded as were number of cells entered and time spent in each (less than a minute, 1-2 minutes, 2-3 minutes, etc.).

Statistical procedures

Section A of the results examines differences between worker-worker and worker-queen interactions. Much of the data is in the form of proportions or relative frequencies (these have sometimes been converted to percentages). The test most frequently employed for detecting significant differences in these proportions was Wilcoxon's matched-pairs signed-ranks test. This was used in the following way. Proportions were calculated by dividing the number of times workers in a nest exhibited a particular behavior (turn arounds, passes, etc.) by the number of times they approached or were nudged by other bees (the proportion analyzed in subsection 3 is an exception to this). Interactions with queens were considered separately from those with other workers. For each behavior of interest (e.g., turn arounds following approaches), a difference score was calculated by subtracting the proportion of times workers exhibited this behavior towards other workers from the proportion of times this behavior was exhibited towards the queen. Nests were arbitrarily eliminated from consideration if the number in the denominator of either proportion was less than 10. Consistency in difference scores across nests was analyzed with the Wilcoxon test.

The Wilcoxon is not strictly appropriate for testing more than one outcome of an interaction for significant differences. This is because the relative frequencies of the different behaviors a bee can exhibit in an interaction are not independent.

In subsections 4 and 5 it was necessary to test two responses to nudging of the head (turn arounds and retreats) for significant differences. The average percentage of nudges by queens and workers that were followed by either turn arounds or retreats in nests 10-17 was 15 % and 13 %, respectively. Since these percentages are low, differences in one behavior are not apt to have a substantial influence on the magnitude and direction of differences in the other. For this reason, the Wilcoxon was employed for testing each of the two categories of behavior for significant differences.

In a few cases the X^2 test was used instead of the Wilcoxon. This method was employed if (1) data from nests had to be combined because the number of observations in each nest was low or (2) the number of times three or more behaviors were exhibited relative to one another was of interest instead of the relative frequency of one behavior.

Sections B, C, and D examine behavioral differences between queens and workers. The data in these sections are in the form of frequencies, proportions, or actual counts. Individuals in each nest were ranked on the basis of these measures; the observed distribution of ranks was then compared to that expected by chance.

RESULTS

A) Avoidance of the Queen

Behaviors that result in avoidance or withdrawal from interactions with other bees include turn arounds (following either an approach or double approach or after being nudged on the head), double turn arounds, and retreats. Several of these behaviors are exhibited by workers more frequently in interactions with queens than with other workers.

1) The mean percentage of approaches to queens and workers that resulted in turn arounds, passes, and following in nests 10-17 is shown in *table I a.* Excluded from this table are those approaches in which the stationary bee nudged the moving bee. Such interactions are included elsewhere under nudging of the head.

Table Ia. — Behavior of workers after approaching stationary nestmate: means for nests 10-17.

Tableau Ia. — Comportement d'ouvrières venant de s'approcher d'autres individus non-mobiles du même nid : moyennes pour les nids 10-17.

Caste of stationary bee	Number of approaches	Percent turn arouds	Percent passes	Percent follows	Percent all other categories
Queen	98.13	37.45	23.25	18.84	20.48
Worker	125.00	11.14	74.79	0	14.06

Table Ib. — Response of stationary bee to approaching worker: means for nests 10-17.

Tableau Ib. — Réponse d'une abeille non-mobile à une ouvrière qui s'approche : moyennes pour les nids 10-17.

Caste of stationary bee	Number of approaches	Percent backs	Percent no responses	Percent nudges	Percent all other categories
Queen	105.00	50.98	31.19	8.21	9.70
Worker	126.38	6.38	85.68	3.13	4.81

Table Ic. — Behavior of workers after approaching stationary nestmate: means for nests 10-17. Included are only those approaches for which a no responses was scored for the stationary bee. Percentages are calculated on the basis of these approaches only.

Tableau Ic. — Comportement d'ouvrières venant de s'approcher d'individus non-mobiles du même nid : moyennes pour les nids 10-17. Nous n'avons pris en compte que les approches dans lesquelles aucune réponse n'a été notée chez l'abeille non-mobile. Les pourcentages sont calculés sur la base de ces seules approches.

Caste of stationary bee	Number of approaches	Percent turn arounds	Percent passes	Percent all other categories
Queen	36.63	48.28	30.11	21.61
Worker	115.13	9.16	79.46	11.40

A higher proportion or approaches to queens than to workers were terminated by turn arounds ($p = .004$, Wilcoxon test). Examination of other proportions shows that workers in each nest are passed more often than queens and that backing-following is limited to worker-queen interactions.

Since an approach involves two bees, one stationary and one moving, the above difference in proportion of turn arounds may be due in part to the behavior of the stationary bee as the other bee approaches it. Queens do, in fact, back much more often than workers when another bee approaches (see *table I b*). Conversely, queens show fewer no responses than do workers.

The responses of queens and workers were significantly different within each nest ($p < .01$, X^2).

If only those approaches that elicited backing by previously stationary bees are compared, it is apparent that differences in the proportion of turn arounds are associated with more frequent backs by the queen. Over 18 % of all approaches to queens involved a turn around preceded by backing; the corresponding figure for approaches to workers was only 2 %. That the entire difference in proportion of turn arounds to queens and to workers cannot be attributed to different frequencies of backing is seen by examining only those approaches to which the stationary bee exhibited no response (*table I c*). Even in the absence of a response from the stationary bee, workers still executed a higher proportion of turn arounds when this bee was the queen than when it was another worker ($p = .004$, Wilcoxon test).

2) A higher percentage of turn arounds by workers was recorded for double approaches involving a queen and a worker (19.4 %, $n = 170$) than for those involving two workers (6.0 %, $n = 168$). Turn arounds by queens were infrequent (1.8 %). Workers passed one another more often than did queens and workers (84.5 % as compared to 55.9 %). Behaviors in the remaining categories were recorded less often for workers than workers and queens (9.5 % as compared to 24.7 %). A X^2 test of these differences is significant at the .01 level. Data from nests 10-17 are combined owing to the low frequency of observation of this behavior. Turn arounds preceded by nudges are considered in the section on nudging of the head.

3) Double turn arounds were seen in 14 of 17 nests. To determine whether this behavior was more frequent when the queen rather than a worker was the nudger, the number of double turn arounds was divided by the sum of turn arounds and double turn arounds. This, rather than total number of abdominal nudges, was chosen as the denominator because a bee contacted on the abdomen is presumably more likely to recognize the caste/identity of the nudger after its antennae are facing the nudger (i.e., after turning around once). The mean value of this proportion for episodes in which the queen was the nudger was .116 ($n = 12$ nests); the corresponding value for episodes in which workers were nudgers was .009 ($n = 12$; two nests in which the denominator of the proportion for either worker- or queen-initiated interactions was less than 10 were excluded from the analysis). A Wilcoxon test of these differences is significant at the .005 level.

4) Another response to nudging that could be classified as avoidance behavior is turning around after being contacted on the head. The proportion that was tested to determine if workers respond differently to queens as compared to other workers was the number of turn arounds divided by the number of nudges to the head. No significant differences were found in turn arounds to queens and to workers (Wilcoxon test).

5) Retreating after being nudged on the head results in greater distance between the contacted bee and the nudger. Comparison of retreats by workers after being nudged on the head by queens as opposed to other workers shows no significant differences when the data are analyzed as in paragraph 4 above.

Retreating also includes moving away after being nudged on the abdomen. When the ratio of number of such retreats to the total number of abdominal nudges is analyzed by the Wilcoxon test, no significant differences are found between worker-worker and worker-queen interactions.

6) More sequences of backing-following were terminated by workers turning around (37.3 % ; $n = 437$) than by queens doing so (1.1 %). While not bearing on differences between worker-worker and worker-queen interactions, this seems another indication that workers frequently avoid or withdraw from interactions with the queen.

B) Guarding and Sitting near the Nest Entrance

The identity of the guarding bee changes frequently in the early stages of ontogeny of the colony (Buckle, in prep.). The following data concern the tendency of the queen to be the last (farthest from the nest entrance) bee in the queue.

For each bee a ratio was calculated of time spent as the last bee in queues of two or more bees, to total time spent in queues. The denominator of this proportion was obtained by subtracting time spent either as a solitary guard or as a lone bee farther inward in the tube from total time spent guarding of sitting near the nest entrance. The mean value of this ratio was .72 for queens and .29 for workers. The data were tested for significance by ranking each bee within a given nest. The bee with the highest ratio was assigned the rank of one.

In 15 of 17 nests, the queen was the highest ranked bee. In one nest of six bees (nest 2) she was the second-ranked bee, whereas in another six-bee nest (nest 15 in which the social structure appeared to be disintegrating) she was the lowest ranked individual. The probability of queens being ranked first in 15 to 17 nests is highly significant by Fisher's Method of Randomization ($p < .0001$).

Overall, queens spent slightly less time sitting in the entrances tubes than did the average worker. The mean proportion for queens was 31 % of total time observed as compared to 37 % for workers. Values for queens varied between 14 and 55 % ; those for workers, between 0 and 69 %.

The identities as well as the relative positions of bees in queues rarely remained constant for more than a few minutes at a time. Changes occurred as individuals either joined or left the queue or switched positions with one another. The factors that contributed to queens spending relatively more time as the last bee in the queue are as follows :

1) Queens often backed when approached by another bee. Thus, when in front of one or more nestmates in the queue, queens frequently backed under these bees as another colony member approached from the direction of the nest entrance. Often queens ended up at the back of the queue where they seemingly awaited the arrival of the approaching bee. If the approaching bee did not follow, as was often the case, queens usually stayed at the back of the queue rather than moving outward to their prior position.
2) Queens made frequent trips between the tube and the nest interior. As a result, queens sometimes spent little time in front of other nestmates. Upon returning to the nest entrance, more often than not they became the last bee in the queue.
3) Queens in the queue in other than the innermost position sometimes turned around and passed the bees behind them. Then, instead of continuing down the tunnel, they often turned around again and remained at the back of the queue.

C) Sitting Elsewhere in the Nest

Queens sat in the outer two-thirds of the main tunnel facing the nest entrance more frequently than workers. Seven of eight queens were observed to sit in this location as compared to nine of 33 workers. The average proportion of minutes that queens spent sitting in such a position was .024 ($n = 8$); the average for workers was .004 ($n = 33$). Queens ranked highest in six of the seven nests. Such an extreme distribution of ranks, using Fisher's method of randomization, is significant at the .001 level.

Queens also sat near other nestmates more than did workers. Examples of this behavior include the following: sitting within one centimeter of a bee that is working or grooming, sitting within one centimeter of an inactive bee that is facing away, and sitting in the burrow outside a cell that another bee is in. Not included in this category are instances of " facing each other " in which two bees, both inactive for the most part, sit head-to-head. Such behavior was characteristic only of young bees (1-3 days old) or of a young and old bee (BUCKLE, in prep.).

Six of eight queens and two of 33 workers were observed sitting near nestmates. The average proportion of minutes that queens engaged in this behavior was .013 ; the corresponding figure for workers was less than .001. Queens ranked highest in all six nests. The probability of a distribution such as this occurring by chance is less than .001 (Fisher's method of randomization).

Four of eight queens as compared to one of 33 workers sat either at junctions of the main tunnel and side burrows or at forks of the main tunnel. Though queens ranked highest in all four nests, caste differences in rankings are not significant if one includes all eight nests in the analysis.

D) Visits to Cells

While in tunnels, queens made more brief visits to cells than workers did. Brief visits are episodes in which a bee spends less than two minutes in a cell or merely puts its head into one. The results were analyzed by ranking the bees within a nest as to the number of brief visits made during a single observation session. Data for each nest could not be summed over days because (a) all bees were not added to a nest at the same time and (b) the number of cells increased over time. There were a total of 71 observation sessions of nests 1-9 when cells were present. Average colony size was 4.92 adults. Queens ranked highest in brief visits in 53 sessions, a significantly higher number than is expected by chance ($X^2 = 126.39$, $p. < .001$).

DISCUSSION

The results presented in section A indicate that workers avoid queens more than they do other nestmates in certain contexts — when approaching a queen and after turning around in response to being contacted on the abdomen. Additional data show that workers turn around in back-follow sequences a large proportion of the time.

Avoidance of more dominant individuals is well-known in many groups of social insects, particularly in the more primitive ones where levels of overt aggression are higher. Subordinate *Polistes* wasps, for instance, either turn away from more dominant individuals or become immobile in their presence (PARDI, 1948 ; WEST-EBERHARD, 1969). Bumblebee workers retreat rapidly from the queen when caught stealing egg (HUBER, 1802, cited in WILSON, 1971). They also tend to avoid direct contacts with the queen and retreat after they approach her (RÖSELER and RÖSELER, 1977). Queen control in highly advanced groups is based largely on nonaggressive signals rather than " brutish dominance " (WILSON, 1971). Workers in these species usually do not avoid queens, though SAKAGAMI and ZUCCHI (1977) report that worker stingless bees retreat hurriedly after being approached by the queen.

Since the queen is the principal nudger in *L. zephyrum* colonies, workers in this species may avoid the queen to keep from being nudged. MICHENER and BROTHERS (1974) have suggested that the queen's frequent nudging may inhibit development of workers' ovaries. If it is true that nudging inhibits ovarian development, it would be to a worker's advantage to avoid being nudged in order to attain a certain degree of ovarian development. Then, in case of death of the queen, the worker would be in a better position to become the replacement queen, especially if its ovaries were larger than those of most other nestmates. [BROTHERS and MICHENER (1974), in their study of queen replacement, found that the worker with the second largest ovaries usually became the new queen.] Among groups of sisters, the role of the replacement queen would be an advantageous one because daughters and sons would be reared (assuming the queen lays all the female and male producing eggs) instead of nieces and nephews.

Many approaches to queens resulted in turn arounds by workers in the absence of any observable response by queens. Since no contact occurred between the individuals, it appears that workers in such situations are responding to chemical cues produced by and unique to the queen that are functional over short distances. The queen's individual odor or a general queen odor may be involved.

The results in section B show that queens spend much time sitting near the nest entrance and that they tend to sit at the back of the queue that forms there. Near the nest entrance, the queen is in an ideal position to intercept returning foragers and lead them to cells being provisioned (see BREED and GAMBOA, 1977).

A queen in the last position is probably less likely than others in the queue to become involved in keeping out predators. There she also has unimpeded escape to the back of the nest in case of some disturbance. Laboratory observations indicate queens often retreat rapidly from the tube when the nest is disturbed. In the field they are typically the last bees removed from nests, being found at the very ends of the burrows (C.D. MICHENER and L. GREENBERG, personal communications).

In the last position in the queue the queen may also be able to control the movements of bees between the front and back of the nest. She can allow workers to pass or not, or she can lead workers to parts of the nest where digging or cell construction are needed.

The results in section C indicate that queens spend more time than workers sitting in the outer two-thirds of the main tunnel facing the nest entrance. The function of sitting in this part of the nest would seem similar to that of sitting at the back of the queue. This is especially likely since much of the time queens sat just one or two centimeters behind the tube. Here, the queen is able to meet returning foragers as well as control the movements of bees between the front and back of the nest. Queens sitting in the tunnel, for instance, were observed to nudge repeatedly bees returning from the tube until they turned around and went back to the entrance. Another location where a queen could exert considerable influence over the movements of other bees would be at branch points in the tunnel. Queens sat in such locations more frequently than workers, but the difference was not significant.

Queens also sat near nestmates more often than did workers. Those episodes which were preceded or followed by bouts of nudging (many were not) may have been periods of inactivity between aggressive interactions with nestmates. Otherwise, it may be that the presence of the queen near a worker acts to deter the worker from moving to another part of the nest (as when the queen is outside a cell that a bee is working in) or decreases the probability that the worker will become inactive (if, for instance, the queen preferentially nudges inactive bees and the bees learn to associate inactivity with being nudged when the queen is nearby). It is also possible that the sitting queen is gathering or waiting to gather information on the amount of progress the worker has made in cell construction, provisioning, etc.

Sitting behind a bee that is inactive probably has a different function, if indeed, one exists. Typically in such instances, both bees are facing outward, with the queen behind a worker. The queen may thus gain protection ; she is also in position to guide the other bee down the tunnel if the latter turns around and faces her.

The results in section D show that queens made more brief visits to cells than did workers. What bees are doing during these brief visits is unknown. It was frequently evident that individuals on brief visits did not work, but simply inspected cells. Colony members, and particularly the queen, may be gathering information on the status of the different cells, determining which ones are ready to be provisioned, which ones are not yet completed, etc. Perhaps this information is later used by the queen to guide or re-direct workers or to influence her own activities, e.g., in shaping the pollen balls and laying eggs. A similar function, i.e., gathering information on what work needs to be done in the nest, has been attributed to patrolling by worker honeybees (LINDAUER, 1961).

As recently as 1974, *L. zephyrum* was described by MICHENER as a species in which primitively eusocial behavior is weakly developed and continuous variation exists in female behavior and physiology, i.e., there are not two isolated castes. BROTHERS and MICHENER (1974) subsequantly showed that queens and workers are more distinct than suggested by the above description. The differences between queens and workers described in the present paper provide additional evidence of the distinctness of the two castes. Furthermore, in a study just completed (GREENBERG and BUCKLE, in prep.), caste differences were found in receptivity to mating. Queens were willing to mate, whereas most workers were not.

The large number of behavioral differences between queens and workers is somewhat surprising, given that primitively eusocial behavior is not well developed in *L. zephyrum* and morphological differences between the castes are either absent or minimal. Selection has evidently favored a significant division of labor between the castes. The existence of guards, foragers, and a third class of more generalized individuals (BROTHERS and MICHENER, 1974) is indicative of a further division of labor among workers. This opportunity to specialize in different tasks is one of the major advantages of group living. The extent of division of labor in *L. zephyrum*, considering the primitive nature of its societies and the fact that many species in its subgenus are solitary, suggests that role specialization may occur early in the evolution of sociality.

The queen's role in *L. zephyrum* colonies seems to be in part that of an organizer or coordinator. Unfortunately, no other species of primitively eusocial bees have been studied as extensively. Investigations of the queen's role in coordinating or directing worker activities in species of varying degrees of primitive eusociality would be of considerable interest. With comparative data at hand, hypotheses could be formed concerning the possible steps in the evolution of mechanisms of social integration.

ACKNOWLEDGEMENTS. — I would like to express my thanks to Drs. Charles MICHENER, Rudolf JANDER, and William BELL and to F. Cole GILBERT and Les GREENBERG for their comments on preliminary drafts of this paper. This work was supported by NSF grant BNS 78-07707, Dr. Charles MICHENER, principal investigator. This is contribution number 1743 from the Department of Entomology, University of Kansas, Lawrence, Kansas, 66045.

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