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POLLEN HOARDING AND USE BY HIGH AND LOW POLLEN-HOARDING HONEYBEES DURING THE COURSE OF BROOD REARING[1]

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Summary

Honeybees (*Apis mellifera*) from a line which had been selected for high pollen-hoarding behaviour (HPH) hoarded more pollen than bees from a low pollen-hoarding line (LPH) when they were kept in observation colonies with known amounts of brood. These differences were not found when brood was in the egg stage and pollen stores were small, but were large and significant when brood was in the larval stage and pollen stores were more abundant. Differences in amounts of stored pollen that were established between the lines during the larval stage were maintained after brood cells were capped, but amounts of pollen stored did not change significantly. HPH bees also hoarded more pollen in the absence of brood. The two lines used similar amounts of pollen and reared similar amounts of brood. Mortality of the LPH bees was higher and varied significantly more than that of the HPH bees. It is suggested that bees which hoard a large amount of pollen are either less inhibited from collecting pollen by the presence of stored pollen or more stimulated to collect pollen by its absence.

Introduction

Pollen is essential to the honeybee because it is its chief source of protein, fats and minerals. The amount of pollen collected by a colony is related to the amount of brood it has (Filmer, 1932; Louveaux, 1950; Fukuda, 1960), especially the amount of unsealed brood (Free, 1967; Todd & Reed, 1970). Mackensen and Nye (1966) demonstrated the heritable nature of pollen-collecting behaviour when they, by selection, successfully established lines of honeybees that collected high and low percentages of alfalfa pollen. In the sixth generation, bees of the high and low lines had 86% and 8%, respectively, of their pollen foragers collecting alfalfa pollen (Mackensen & Nye, 1969).

Two-way selection for high pollen-hoarding (HPH) and low pollen-hoarding (LPH) bees was begun at The Ohio State University Bee Laboratory during spring 1979. Four generations of selection produced lines of honeybees with significantly different high and low pollen-hoarding behaviour (Hellmich et al., 1985). Fourth generation HPH colonies averaged from two to thirteen times as much stored pollen as the LPH colonies when they were monitored from July to October.

The following experiment was made at The Ohio State University Bee Laboratory to investigate the effect of certain factors on the pollen-hoarding behaviour of the two lines. The objectives were: (1) to compare the amounts of pollen stored by HPH and LPH line colonies during the egg, larval and post-capping stages of brood rearing; (2) to determine whether colonies from the two lines use different amounts of pollen.

Materials and Methods

Twelve colonies of HPH and twelve of LPH bees were used. Each colony contained approximately 1000 newly emerged bees obtained by allowing several frames of capped brood to emerge overnight in an incubator, and a mated queen, randomly selected from miscellaneous stock, confined to a screen cage. Four observation colonies from each of the two lines were housed in an observation-hive shelter during each trial. Three trials were conducted in three separate shelters, each of which had sides facing north, south, east and west. One HPH colony and one LPH colony were placed on each side of each shelter. The first trial was started on 29 April, the second on 1 May, and the third on 3 May.

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At the beginning of each trial, when the bees were approximately 15 days old, dark comb with 400 eggs (0-40 h old) was put into each of the eight observation colonies. Eggs were obtained by confining a queen from miscellaneous stock on an empty comb with a queen-excluder cage. Any extra eggs were crushed before combs were put into the colonies. Each trial lasted a total of 27 days through two cycles of brood rearing (which included the egg and larval stages, and three days after brood cells were capped) and a five-day interim period in which colonies were given dark combs with no brood and no food stores.

In every colony the cells with stored pollen were counted each morning before foraging started, and each evening after foraging stopped. The amount of pollen used overnight was deduced by subtracting the number of cells containing pollen at the morning observation from the corresponding number at the previous evening observation. This is not a precise measure of pollen use, because the bees might eat pollen from many cells without emptying them, but it should be a good relative measure if the two lines emptied cells of pollen in a similar manner. After each trial, the bees remaining in each colony were frozen and then counted for a measure of bee mortality.

A two-level factorial design was used for analysing brood reared and mortality data. Line (HPH and LPH) and trial (1, 2 and 3) were used as grouping factors. A rank transformation on the mortality data was necessary because of non-homogeneity of line variances. For the pollen-use analysis, a three-level factorial design was used in which line, trial and direction (north, south, east and west) were used as grouping factors. Direction and trial groupings were used only to account for variation due to these factors. For the hoarded-pollen analysis, daily measures were nested within line, trial and direction, and repeated measures analysis for days was used for a line-by-day trend analysis. This analysis allows one to describe statistically daily changes in amounts of pollen hoarded by the two lines. The Greenhouse-Geisser procedure (G.G.) was used to adjust degrees of freedom for the line-by-day interaction to account for consecutive-day dependence. When the G.G. statistic was significant, orthogonal polynomials [line (l) × day (l) and line (l) × day (q); where (l) = linear and (q) = quadratic] were partitioned from the sum of squares of the line-by-day interaction. Only the statistics from the orthogonal polynomials are given in the text. (For details concerning Greenhouse-Geisser procedure see Winer, 1962).

Results and Analyses

A. Pollen use

Similar amounts of pollen were used by the two lines throughout most of the experiment (Fig. 1), though HPH bees used more pollen during days 16 ($P<0{\cdot}02$), 19 ($P<0{\cdot}03$) and 22 ($P<0{\cdot}01$) and LPH bees used more during day 24 ($P<0{\cdot}0002$). These differences were not the same from one cycle to the next and did not follow a consistent pattern.

B. Pollen hoarded by the two lines

1. First cycle of brood rearing

During the egg stage, days 1 and 2, there were no significant differences between HPH and LPH bees in amounts of pollen stored (Fig. 2).

However, during the first half of the larval stage, days 3–5, the HPH line had larger amounts of pollen in store than the LPH line ($P<0{\cdot}05$). The trend analysis indicates that during this time the high pollen-hoarding bees were hoarding pollen faster than the low pollen-hoarding bees. Differences between the lines increased in a linear fashion [line (l) × day (l); $P<0{\cdot}005$], because the HPH colonies were storing more pollen than they consumed and the LPH colonies were not (Fig. 1, Fig. 2).

High pollen-hoarders had larger amounts of pollen stored than low pollen hoarders during the second half of the larval stage also — days 6–8 ($P<0{\cdot}005$). The trend analysis in this case indicates that the amount of pollen in the LPH line colonies decreased faster than that in the HPH line colonies [line (l) × day (l); $P<0{\cdot}04$].

During the first three days after brood cells were capped, i.e., days 9–11, high pollen hoarders still had more pollen in store than low pollen hoarders ($P<0{\cdot}002$) and the difference remained similar to that reached between lines during the larval stage. This is indicated by a non-significant line-by-day interaction for this period.

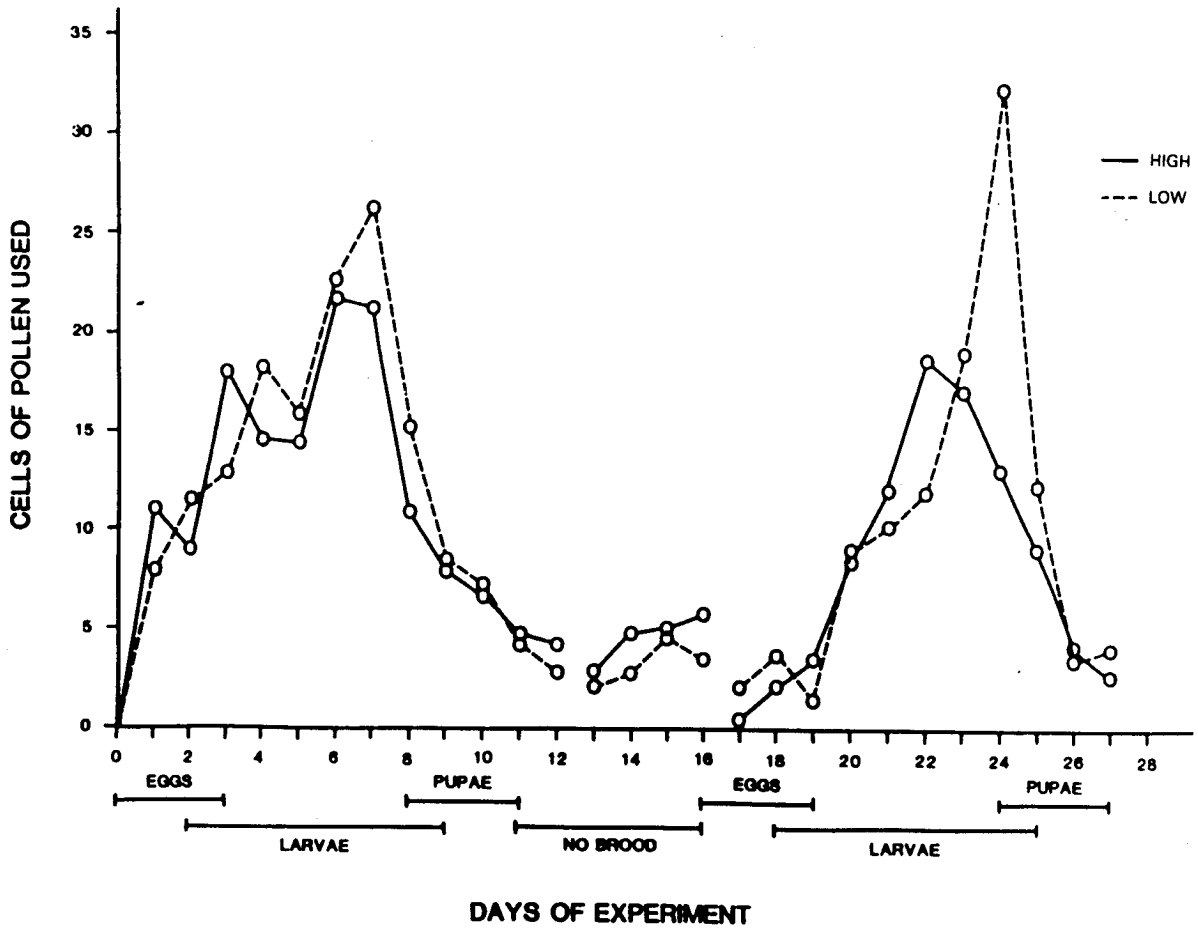

FIG. 1. Mean number of cells of pollen used by 12 high pollen-hoarding and 12 low pollen-hoarding colonies observed each day through two cycles of brood rearing and a broodless period.

2. Broodless period

During the five-day broodless period, days 11–16, high pollen hoarders again stored larger amounts of pollen than low pollen hoarders (Fig. 2; $P<0{\cdot}001$). Thus, the trend analysis shows that the amount of pollen the high pollen-hoarding bees had in store increased faster than that of the low pollen-hoarding bees. Differences between the lines increased in a nearly linear fashion till day 13 [line (l) × day (l); $P<0{\cdot}03$] but began to level off later [line (l) × day (q); $P<0{\cdot}04$].

3. Second cycle of brood rearing

There were no significant differences between HPH and LPH lines in amounts of pollen hoarded during the egg stage, days 17 and 18 (Fig. 2).

During the first half of the larval stage, days 19–21, HPH and LPH lines hoarded similar amounts of pollen. However, during the second half of the larval stage, days 22–24, ($P<0{\cdot}05$) and during the first three days after brood cells were capped, days 25–27, ($P<0{\cdot}008$) high pollen hoarders once again had more pollen in store than low pollen hoarders. The line-by-day interaction is not significant for either of these periods, which indicates that relative differences between lines did not change appreciably during them.

4. Comparison of first and second cycles of brood rearing

Both lines of bees appeared to store less pollen in Cycle Two than in Cycle One. This difference in amount of pollen stored may be due to fewer bees being alive in Cycle Two, bees

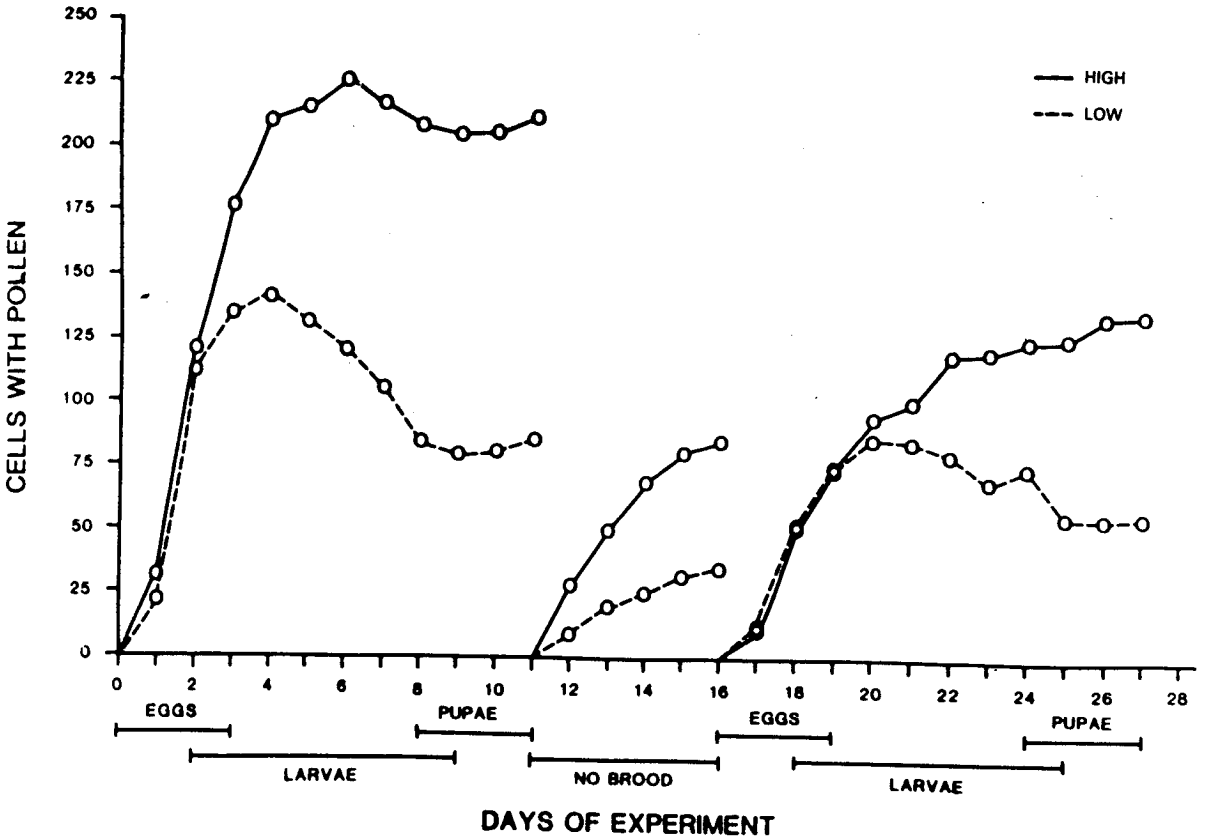

FIG. 2. Mean number of pollen cells for 12 high pollen-hoarding and 12 low pollen-hoarding colonies observed each evening through two cycles of brood rearing and a broodless period.

being older in Cycle Two, previous experience in Cycle One of bees in Cycle Two, or some environmental factor such as availability of pollen. Because of uncontrollable random differences between the cycles, no further analysis is possible.

C. Brood reared

Amounts of brood reared by the two lines during the first [$\bar{x}_{(HPH)} = 330 \pm SE\ 89$; $\bar{x}_{(LPH)} = 277 \pm SE\ 110$] and the second [$\bar{x}_{(HPH)} = 282 \pm SE\ 87$; $\bar{x}_{(LPH)} = 262 \pm SE\ 76$] cycles of brood rearing were not significantly different. Amounts of brood reared during the two cycles [$\bar{x}_{(cycle\ 1)} = 304 \pm SE\ 101$; $\bar{x}_{(cycle\ 2)} = 272 \pm SE\ 80$] also were not significantly different.

D. Worker Mortality

More high pollen-hoarding bees [$\bar{x}_{(HPH)} = 591 \pm SE\ 52$] were alive at the end of each trial than low pollen-hoarding bees [$\bar{x}_{(LPH)} = 456 \pm SE\ 101$; $P<0{\cdot}025$]. LPH line bee mortality also varied significantly more than that of the HPH line bees [$s^2_{(HPH)} = 2656$; $s^2_{(LPH)} = 10272$; $P<0{\cdot}05$]. Differential mortality might have affected results from the second cycle of brood rearing—especially towards the end—but was not considered an important factor during the first cycle and the broodless period.

Discussion

The different amounts of pollen stored by the high and low pollen-hoarding lines could be because HPH bees collected more pollen than LPH bees, or LPH bees consumed more pollen than HPH bees. Since pollen use by the two lines was similar, the differences between lines appear to be related only to the amounts of pollen collected. There is no simple way to describe these differences; however, the amount of pollen collected by each line varied considerably

with the stage of brood and amount of pollen present in the colony. At some times the amounts of pollen collected by the two lines were similar, but at other times they were appreciably different.

Four distinctly different brood and pollen-storage combinations occurred during the experiment. In the egg stage and broodless period, the colonies had small amounts of stored pollen, while in the larval stage and post-capping period the colonies had more abundant amounts of stored pollen.

HPH line colonies collected considerably more pollen than LPH line ones during the larval stage, and thus accumulated greater stores of pollen during this period. At this time, when nurse-bee consumption of pollen was great, pollen used by LPH line colonies was often greater than pollen intake. As a result a few of the LPH line colonies had no pollen in store when morning observations were made, and so were dependent upon that day's foraging for pollen. HPH-line colonies at the same time always had cells of stored pollen.

The two lines collected similar amounts of pollen during the egg stage, but it is unclear whether presence of eggs or absence of pollen was more important in eliciting pollen collection. During the broodless period, when pollen stores were low again, HPH line bees hoarded more pollen than LPH line bees. The higher pollen hoarding by HPH line colonies during this period suggests that the two lines responded differently to the presence or the absence of pollen but this difference was suppressed when eggs were present.

Amount of pollen collected and amount of pollen consumed by each of the lines decreased during the post-capping period, presumably because the brood stimuli were reduced. With both lines during this period pollen storage approximately equalled pollen consumption, so the levels of stored pollen, although different between lines, remained unchanged. It seems that HPH line colonies accumulate higher levels of pollen than LPH line colonies by being either less inhibited by the presence of stored pollen or more stimulated by its absence.

Insufficiency of pollen stores of LPH line colonies did not appear to interfere with brood production during this study. However, LPH line bee mortality was higher and more varied than that of the HPH line bees. This may have been related to inadequate pollen stores. Another investigation (Hellmich, unpublished data) suggests that LPH line colony survival can be more reduced than that of the HPH line when there is a dearth of pollen.

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