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CORBICULAR SIZE IN WORKERS FROM HONEYBEE LINES SELECTED FOR HIGH OR LOW POLLEN HOARDING

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Summary

Measurements were made of corbicular areas (of a total of 1025 corbiculae) in 2 lines of honeybees (*Apis mellifera*) selected for high and low pollen hoarding respectively. The sample from each line comprised about 30 newly emerged workers from each of 9 queens representing 3 sublines. Analyses of variance revealed highly significant differences among the 18 queens ($P < 0.0001$) and between the lines ($P < 0.0001$). Mean corbicular area for the high pollen-hoarding line ($1.909 \pm 0.004 \text{ mm}^2$) was greater than for the low hoarding line ($1.874 \pm 0.003 \text{ mm}^2$). Of the 9 queens whose worker progeny had the largest corbiculae, 7 belonged to the high pollen-hoarding line. A Mann-Whitney U-test of rank indicated that the distribution of the queens for the 2 lines differed significantly ($P < 0.05$). Assuming the difference to be genetic, as indicated from a previous heritability estimate, unintentional selection for worker corbicular area must have been performed during selection for divergent pollen-hoarding ability in the colony.

Introduction

In the honeybee colony, pollen is used primarily for brood rearing and is often a limiting factor to colony growth and productivity. Milne and Pries (1984) reported a significant phenotypic correlation between size of worker corbicula (pollen basket) and honey production. Colonies of workers with larger corbiculae produced more honey. Milne (1985a) found that corbicular area and honey production were correlated for two out of three years in which they were measured. This relationship between corbicular area and honey production is somewhat tentative since it is based on phenotypic correlations, and its status would be strengthened if based on the more complex genetic correlations.

An estimate of 1.014 ± 0.195 was obtained for the heritability (h^2) of corbicular area, indicating that most, if not all, of the phenotypic variation has a genetic origin (Milne, 1985b). Milne and Pries (1984) hypothesized that the larger corbiculae enabled larger pollen loads to be carried, so that the larger pollen income might be used either to raise more or longer-lived adults, or to free some workers to collect nectar. Subsequently Milne and Pries (1986) demonstrated that workers with larger corbiculae carry larger pollen pellets.

Hellmich et al. (1985) successfully selected for high and low pollen hoarding in the colony. Two divergent lines, which differed significantly during each of the four generations of selection in their pollen-hoarding ability, were developed using direct measurements of pollen stored in the combs. The high pollen-hoarding line stored significantly more pollen than the low line. Each line was maintained as three sublines. During selection, h^2 for divergence for pollen hoarding was estimated to be $49.5 \pm 20.3\%$.

The present study was initiated to examine corbicular area in workers of these high and low pollen-hoarding lines to determine whether unintentional selection for corbicular area occurred during selection for divergence in pollen-hoarding ability.

Materials and Methods

Corbicular areas were determined for approximately 30 dried, newly emerged worker progeny of each of 18 queens, both corbiculae being measured in each individual. Nine queens were from the line selected by Hellmich et al. (1985) for high pollen-hoarding and nine were from their low pollen-hoarding line. Each line was maintained in three sublines and the nine queens from each line comprised three queens from each subline. The semen of one drone was used to

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inseminate each queen, and the queens were from the 4th selected generation.

Milne and Pries (1984) have described in detail the corbicular area measurements. A stereo-dissecting microscope with a calibrated micrometer reticule fitted into one eyepiece was used to measure length and width of the triangular corbicula, and the area was calculated as half the product of length and width. The person measuring the corbiculae did not know whether an individual bee belonged to a high or low pollen-hoarding line.

Results

Mean corbicular areas for workers of each of the 18 queens and their ranks within the group are listed in Table 1. A total of 1025 corbiculae was measured. Analysis of variance revealed highly significant differences among queens for corbicular area ($F = 32.16$, $df = 17$ and 1007 , $P < 0.0001$). A Duncan's multiple-range test identified the differences among the queens. Seven of the nine queens whose worker progeny had the largest corbiculae were from the high pollen-hoarding line and seven of the nine queens whose workers had the smallest corbiculae were from the low line. A Mann-Whitney U-test of rank revealed that the distributions of queens for the two lines were significantly different ($U = 21$, $P < 0.05$).

The average worker corbicular area ($\bar{x} \pm SD$) for all the high pollen-hoarding lines was $1.909 \pm 0.004 \text{ mm}^2$. This was larger than that for the workers of the low pollen-hoarding lines ($1.874 \pm 0.003 \text{ mm}^2$). An analysis of variance revealed highly significant differences between the two lines ($F = 50.68$, $df = 1$ and 1023 , $P < 0.0001$).

TABLE 1. Corbicular areas for worker honeybees from queens in lines selected for high (H) and low (L) pollen hoarding.

Differences among queens and between lines were significant in analyses of variance at $P < 0.0001$. Means followed by the same letter are not significantly different by Duncan's multiple-range test ($\alpha = 0.05$).

Rank	Queen	Line	No. corbiculae measured	Corbicular area (mm^3)
1	6	H	57	1.986a
2	17	H	58	1.984a
3	2	L	58	1.961a
4	13	H	57	1.918b
5	1	H	57	1.915b
6	10	H	57	1.910bc
7	5	H	54	1.904bc
8	8	H	60	1.904bc
9	16	L	60	1.892bcd
10	12	L	60	1.886cd
11	7	L	58	1.873de
12	14	L	45	1.873de
13	11	L	60	1.866def
14	15	L	54	1.850efg
15	4	H	59	1.842fgh
16	18	L	56	1.831gh
17	3	H	58	1.828gh
18	9	H	57	1.822h

Discussion

Workers from the line selected for increased pollen hoarding had significantly larger corbiculae than those from the low line. Although deliberate selection was only for increased or decreased pollen hoarding in the colony, it appears that inadvertent selection had been exercised for corbicular area as well. This finding, along with the results of Milne and Pries (1986) showing that workers with larger corbiculae carry significantly larger pollen pellets, supports the idea of Milne and Pries (1984) that colonies of workers with larger corbiculae are able to bring more pollen to the colony.

An alternative explanation could account for these results. The workers measured in this study were reared in colonies headed by their queens and populated by their sisters. Workers

from the high pollen-hoarding line came from colonies with a significantly larger pollen income than the low line. Therefore, the environmental conditions of the workers prior to emergence differed significantly between the two lines. If extra pollen results in larger adults with larger corbiculae, then the workers from the high pollen-hoarding line would have larger corbiculae. This would be consistent with the results of Eischen et al. (1982) and Milne and Friars (1984), which show that environmental conditions can influence worker size. Milne (1985a) reported a significant phenotypic correlation between corbicular area and size, which suggests, though it does not prove, that larger workers have larger corbiculae. A significant genetic correlation would be needed to prove the relationship.

It is possible to test this explanation directly by rearing brood from high and low pollen-hoarding lines under the same environmental conditions. Brood from both lines could be reared in the same colony at the same time on adjacent frames, thus making conditions after the egg stage nearly the same. This would make conditions for the two lines more similar than those used in the present experiment.

But this explanation using environmental conditions is rendered improbable by one recent observation. Milne (1985b) estimated that h^2 for corbicular area in a population of 73 free-mated queens was about 1.0. If the pollen income in a colony influences the corbicular size, then h^2 for corbicular area would be less than 1.0 for this population. The estimate of 1.0 argues that all the phenotypic variation observed for corbicular area is genetic in origin. Therefore, if the results from the population of 73 free-mated queens are extended to those of the two lines used in this experiment, environmental conditions before emergence should have little or no influence on worker corbicular area.

The differences between the amounts of pollen hoarded by the high and low lines was, in several cases, much greater than 100% (Hellmich et al., 1985). But the difference between the mean corbicular area for the two lines was around 2%. Several factors may account for this finding. In their selection programme corbicular area was not the object of selection and was only improved incidentally. The naturally occurring variation for corbicular area in a normal population is much less than for the amount of stored pollen. Finally, corbicular area is probably only one element of many improved by selection for increased pollen hoarding.

Worker corbicular area is one factor contributing to the difference in pollen-hoarding ability between these two selected lines. There are undoubtedly others. For example, the lines may differ in the worker pollen-collecting response to stimuli from brood or returning foragers. Their behaviour in searching for flowers, or on the flowers, may also differ. Finally, hair characteristics may be different so that the high pollen-hoarding workers collect pollen more efficiently.

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