Number of Adult Honey Bees (Hymenoptera: Apidae) Occupying a Comb: A Standard for Estimating Colony Populations

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ABSTRACT   A quantification of the number of adult worker *Apis mellifera* L. found on combs of standard sizes at full holding capacity is reported. Estimating the holding capacity of combs can assist in evaluating honey-bee colonies for pollination capabilities and also for honey-production potentials.

THE ABILITY to estimate accurately the number of adult honey bees (*Apis mellifera* L.) in a colony is valuable in determining the relative capabilities of hives utilized for pollination and, to a lesser extent, for honey production. Adult-population estimates have been derived from gravimetric techniques that involve weighing colonies in toto, followed by the removal of all adult bees and a reweighing of the colonies (Moeller 1958). This technique is both excessively invasive and time consuming. To produce an accurate population estimate, the establishment of a standard unit of population measure is necessary. This has been done by counting frames of adult bees (Simpson 1969, Waller et al. 1985). However, there is no widely accepted standard for the number of adult bees on a frame when it is fully covered, a concept we term the holding capacity of a comb. Simpson (1969) stated that a standard Langstroth deep frame possesses an average of 1,400 adult bees. Because it resulted from a study of space requirements for colony growth and represented the average number of adult bees found on occupied combs, this figure is not the holding capacity of a standard deep comb.

The figure of 1,900 has been presented as the number of adult bees found on a deep comb where the comb is covered on both sides by a single layer of bees (Kauffeld 1975). Preliminary investigations into the holding capacity of deep combs (Burgett et al. 1984) suggested that the figure of 1,900 adult bees is too low. Here we report the results of an expanded study in which we investigated the number of adult worker bees that can be found on a comb at full holding capacity.

Materials and Methods

We calculated comb holding capacity by two methods. First, we constructed a model population for a comb of any given area. This was done by calculating the personal space of an average worker honey bee. The average personal space for an individual worker was defined as the sum of the dorsal surface area and an estimation of the spatial area that separates adjacent bees on a comb. The surface area was determined by measuring samples of worker bees taken from both brood and honey-storage combs. Dorsal length was measured from the frons to the tip of the seventh abdominal tergite, and width was measured across the dorsal surface of the third abdominal tergite. From these two parameters, the dorsal surface area was calculated from a sample of 100 workers. The spatial area separating adjacent workers was assigned an empirical value of 8% of the dorsal surface area.

Comb-surface areas were calculated from measurements of the four frame sizes most commonly used in American beekeeping (e.g., deep, semi [¾'s], western, and shallow). All calculations were made on the surface of comb alone and did not include any area of the wooden frame.

Once the personal space of an individual worker was determined, that figure was divided into the known surface areas of the four comb sizes to determine a model population of adult workers at full holding capacity for each comb size.

A model population was verified for the full frame only through a series of estimation trials, where deep combs were removed from test colonies and an estimated percentage of coverage was made by each of two observers. These independent estimates were averaged for each comb before the final determination of the actual worker population of each comb examined. For ease of estimation, each side of a comb was assigned a value of 100%. The combined worker coverage estimates for both sides of a comb, therefore, represent an estimated percentage of coverage for a total area of 200%, a full comb. Visual estimates of the total area covered by adult workers on a comb side were obtained with a technique similar to one used in plant ecology, where estimates of vegetative coverage are made with small grids (Daubenmire 1959). A similar technique is described by Rogers et al. (1983) for measuring brood
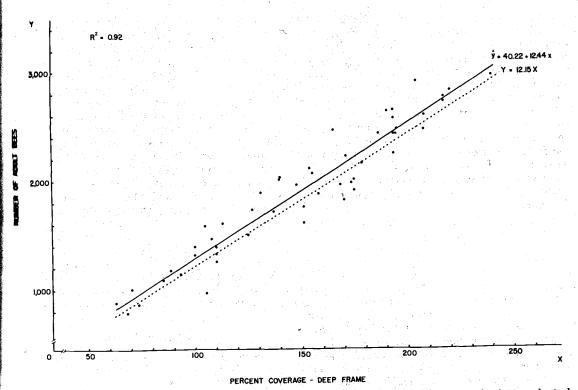
Fig. 1.   (Solid line) Calculated worker bee populations on estimates of coverage. (Broken line) Hypothetical worker bee populations based on a worker personal space of 0.72 cm².

area on comb surfaces. With little experience, the investigator visually divides a comb into quadrants and mentally rearranges the workers to fill the quarters or parts thereof and thereby obtains an estimate of percentage of coverage.

Following coverage estimates, the bees were subjected to carbon dioxide narcosis and weighed to the nearest 0.01 g. Four subsamples of 10 workers each were weighed to calculate the average bee weight for each comb examined. From these data, the total number of bees on the comb was derived. The estimates of coverage with known bee populations were subjected to linear regression analysis. The slope and the intercept of the constructed regression line were tested for significant differences with those of the regression equation

Table 1.   Standard comb areas and adult worker holding capacity

Comb size	Length	Depth	Area[a]	Full holding capacity[b]
Deep	43.1 cm	20.3 cm	1,759 cm²	2,430
¾'s	43.1	15.2	1,310	1,820
Western	43.1	13.1	1,129	1,570
Shallow	43.1	10.7	922	1,280

[a] Computed from length × depth × 2 for double-sided comb.
[b] Comb area only at a worker personal space of 0.72 cm².

generated from the hypothetical population based on the calculated worker personal space and deep comb area. Statistical tests concerning slope and intercept were based on t tests and followed the procedures of Neter et al. (1983).

Results

Table 1 presents the measurements of the four standard combs and the calculated comb areas. Also presented are the hypothetical worker-bee populations at full coverage based on a worker-bee personal space of 0.72 cm². This figure results from the sum of the mean dorsal surface area of 0.67 ± 0.05 cm² ($n = 100$) and an empirical designation of 0.05 cm² as the spatial area separating adjacent workers (8% of the dorsal surface area). A companion calculation is the number of workers per unit area (for our data it is 1.39 worker per cm²). Hypothetical worker populations at full coverage are: deep, 2,430; semi, 1,820; western, 1,570; and shallow, 1,280.

Figure 1 shows the regression lines of known bee populations on estimates of coverage and hypothetical populations based on a calculated worker-bee personal space of 0.72 cm². The fitted regression equation $\hat{y} = a + bx$ of known bee populations on estimates of coverage is, $\bar{y} = 40.22 + 12.44x$ ($n = 51$). There is a linear relation between known bee populations and estimates of

coverage (t test for slope = 0, $P < 0.0005$). The r^2 of 0.92 indicated that estimates of coverage explained ca. 92% of the variation in known bee populations. The regression equation generated from the hypothetical population, $y = 0 + 12.15x$, was calculated from the number of hypothetical worker bees on a deep frame (2,430) divided by full coverage (200%), to obtain the amount of change in the number of bees for each 1% coverage. The slope (12.44) and the intercept (40.22) of the fitted regression line of known bee populations on estimates of coverage have no significant differences from those of the hypothetical line, 12.15 and 0 respectively (t test, slope $P > 0.50$, intercept $P > 0.60$).

Discussion

Errors in accurately estimating colony populations, based on a known standard population of a frame at full coverage, can come from several sources. An obvious error would be inaccurate estimates by a designated observer. Inaccurate estimations can be overcome by combining a series of estimates with gravimetric measures to verify the number of bees on a sample of combs. Also, we recommend that estimates be based on the combined averages of two observers. A second source of error is the bees that occupy areas of the wooden frame in addition to comb surface. In our estimation trials for deep frames, we rarely found more than a few bees occupying the end bars, but with combs at or near holding capacity, the top and bottom bars were frequently occupied by large numbers of bees. The surface area of standard top and bottom bars can add a significant amount to the area of a comb, ranging from a 26% increase for a deep comb to nearly 50% for a shallow comb. To minimize error for bees on frame surfaces, we mentally placed these bees on the comb surface for coverage estimation purposes. A third error can be the presence of drones. If present in significant numbers, drones would produce an overestimation of workers. We calculated the personal space of a drone to be 0.94 ± 0.07 cm^2 ($n = 25$) (i.e., 31% greater than the personal space of a worker). However, the population of drones in normal queenright colonies is small enough that, as a source of error, the number of drones on a series of combs should be minimal. For example, if drones were to occupy 5% of the comb area on a deep comb at full coverage, 94 drones would be present, which would be a worker-bee overestimation of 122 bees. It should also be evident that in a congested colony the worker density can be greater than our defined holding capacity of 2,430 workers per deep comb. A review of the coverage estimates in Fig. 1 shows

a number of combs where estimates were >200% and worker populations >2,430. The application of our technique assumes that temperature and weather conditions preclude flight of the worker forager force during the times the estimates are made. Estimations done when colonies are actively foraging need to take into account the absence of this often substantial subpopulation of worker bees.

In practice, a colony-population estimate is produced by visually examining each comb and estimating the percentage of coverage. At the conclusion of the examination, the percentage estimates for all occupied combs are summed and divided by 200 to produce the number of full-frame equivalents. This number, when multiplied by the worker holding capacity standard for the appropriate comb size, yields an estimate of colony worker population. An accurate worker estimate combined with a brood estimate (Rogers et al. 1983), provides an evaluation of the pollination capability of a single colony, and more importantly, the relative potential of a series of colonies.

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