Complementary Aspects of Strawberry Pollination by Honey and Indigenous Bees (Hymenoptera)

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ABSTRACT The relative efficiency of two groups of insects that pollinate strawberries, *Fragaria* × *ananassa* Duch., was established by comparing the relative influence of the number and length of their visits to flowers, their foraging behavior, and the fertilization rates of the achenes during these visits. Honey bees, *Apis mellifera* L., were more efficient than indigenous pollinators (Hymenoptera: Andrenidae, Halictidae, and Megachilidae) when the frequency of visits was low. Average-sized apoids such as honey bees pivot at the top of the receptacle and pollinate the apical stigmata, whereas small apoids circle on the stamens and around the receptacle, pollinating mainly the basal stigmata. Data collected revealed that these two groups of pollinators play a complementary role in strawberry pollination.

KEY WORDS pollination, strawberries, *Apis mellifera*

COMMERCIAL CULTIVARS OF THE STRAWBERRY, *Fragaria* × *ananassa* Duch., produce hermaphroditic flowers, all of which must be pollinated to yield strawberries of maximum size. Most pollination is done by the combined action of gravity and wind, but the pollination rate of the achenes rarely surpasses 60% if no insect pollen transport occurs (Connor 1970, Pion et al. 1980). Free (1968) and Pion et al. (1980) found strawberry malformation rates of 48.6 and 46.5% in the absence of pollinating insects. Because this type of crop is not especially attractive to pollinators (Darrow 1966), pollinator density may be increased by the introduction of hives of honey bees, *Apis mellifera* L., particularly in areas where monoculture is practiced and commercial strawberries are far away from the nesting sites of natural pollinators (Jaycox 1970, McGregor 1976). The value of this practice, however, in areas where indigenous bee populations are high, has been questioned. Nye & Anderson (1974) evaluated the efficiency of various strawberry pollinators by giving scores based on insect body size, the quantity of pollen accumulated on their body, the level of contact with pistils and stamens, and the length of visits to flowers. In our study, the efficiency of pollinators was measured by the effect of the number and length of visits to flowers on the pollination rate of the resulting strawberries.

Materials and Methods

Observations on honey bee foraging behavior were done from 26 May to 6 June 1985 on 'Veestar' strawberry. Plots were located at the Agriculture Canada Experimental Farm in l'Acadie in southern Québec. Before flowering began, plants from seven randomly selected plots were isolated under gauze (20 meshes) cages (1 by 0.75 by 0.30 m). Six beehives were placed ≈100 m from the experimental plots. Early in the morning, each open flower was tagged. When foraging became intense, one of the cages was opened, after which the comings and goings of the bees were timed and tape recorded, as were notes on foraging behavior. Number and length of visits to flowers were established by tape recordings. When the pollinator could be identified, the species was noted. Unidentified individuals were collected for later species determination. When the observation period was over, the cage was closed to exclude subsequent visits.

After flowering, the gauze was removed. At harvest time, each berry was first weighed. Fertilized and unfertilized achenes were then counted. The pollination rate for each berry was determined by the proportion of fertilized achenes. Results from the experimental plots were compared with two types of controls: strawberries from flowers kept under gauze cages that prevented access for the pollinators throughout

Table 1. Pollinator insects observed on strawberry flowers

Family	Species	Size[a]	No. individuals observed	% Relative abundance	Mean length of first visit, s[b]
Andrenidae	*Andrena lata* Viereck	Medium	1	0.14	—
	Andrena nasonii Robertson	Small	46	6.25	124.9 (± 74.7)
	Andrena wilkella Kirby	Medium	3	0.41	—
Apidae	*Apis mellifera* L.	Medium	530	72.01	24.4 (± 12.5)
Halictidae	*Halictus confusus* Smith	Small	36	4.89	43.2 (± 31.5)
	Dialictus lineatulus Robertson	Small	80	10.87	133.2 (± 54.6)
	Dialictus sp.	Small	2	0.27	—
	Dialictus cressonii Robertson	Small	18	2.45	49.4 (± 20.1)
	Augochlorella striata Provencher	Small	19	2.58	38.8 (± 10.2)
Megachilidae	*Osmia atriventris* Cresson	Medium	1	0.14	—

[a] Small size, <1 cm; medium size, >1 cm.
[b] —, data unavailable.

flowering (caged controls), and strawberries from freely pollinated flowers from open-field plots (foraged controls). Nonparametic tests, such as Spearman correlation, Mann-Whitney *U* test and Kruskall-Wallis test for several independent samples (Sherrer 1984) were used to analyze data. Statistical tests were performed with Number Cruncher Statistical System (Hintze 1989).

Results and Discussion

The 10 insect pollinator species observed, as well as the frequency of their visits, are listed in Table 1. From a total of 736 recorded visits, indigenous bees accounted for 28% and honey bees for 72%. The high frequency of honey bees can be explained by the proximity of the hives to the study plots. The pollinators were divided into two groups according to body length: small size (<1 cm) and medium size (>1 cm). Honey bees belong to the latter.

Behavior of the Indigenous Bees. Six indigenous bee species were small in size and had very similar foraging behavior patterns on the flowers (Table 1). Generally, these apoids landed directly on the stamens. Less frequently, they landed on the petals or the receptacle and later walked to the stamens. They followed a circular path both on and between the stamens (Fig. 1a). They often stopped and rubbed their forelegs alternately on the anthers. This caused the dispersal of pollen as well as a visible accumulation of pollen grains on the leg bristles and on the ventral side of the thorax. While collecting nectar, they plunged their heads and upper thoraces between the basal pistils and the internal row of stamens. Their route was then retraced either in the same or opposite direction while they stayed on the peripheral part of the receptacle. During the same visit, they alternated regularly between pollen and nectar collection. These small bees rarely moved over the center of the flower where the apical stamens are located. However, they did cross over occasionally when a flower had been foraged several times and the search for nectar seemed to become difficult. A disordered path was also observed when a second bee arrived on the same flower. A few bees (Andrenidae and Megachilidae) were slightly larger than these small apoids, and their foraging behaviors were similar to that of honey bees. The number of visits by these species, however, was negligible (Table 1).

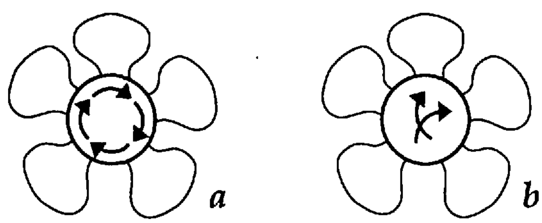

Fig. 1. Schema of the movement of pollinators on strawberry flowers. (a) Indigenous bees. (b) Honey bees.

Behavior of Honey Bees. Honey bees usually landed on the center of the flower and occasionally on the internal section of the perianth near the ring formed by the anthers. Irrespective of their first approach, these bees eventually moved to the central zone of the stigmata. To forage nectar, a given honey bee rocked its thorax and abdomen on the central stigmata, then spread the stamens with its head by inserting its proboscis into the nectaries. It pivoted gently on the flower and then began the process again (Fig. 1b). These repetitive movements appeared to favor pollen fixation on the bee's body, as well as dispersion of autogenous or heterogenous pollen on the stigmata. During a given visit, a forager usually collected nectar, after which it collected pollen.

Length of Visits. The correlation between the accumulated time of visits to flowers and the percentage of fertilized achenes in resulting strawberries for honey bees was significant (r = 0.314, n = 93, P < 0.0001) (Chagnon et al. 1989) but this relationship was not significant for small indigenous bees (r = 0.208, n = 49, P > 0.05). The latter results were predictable because vari-

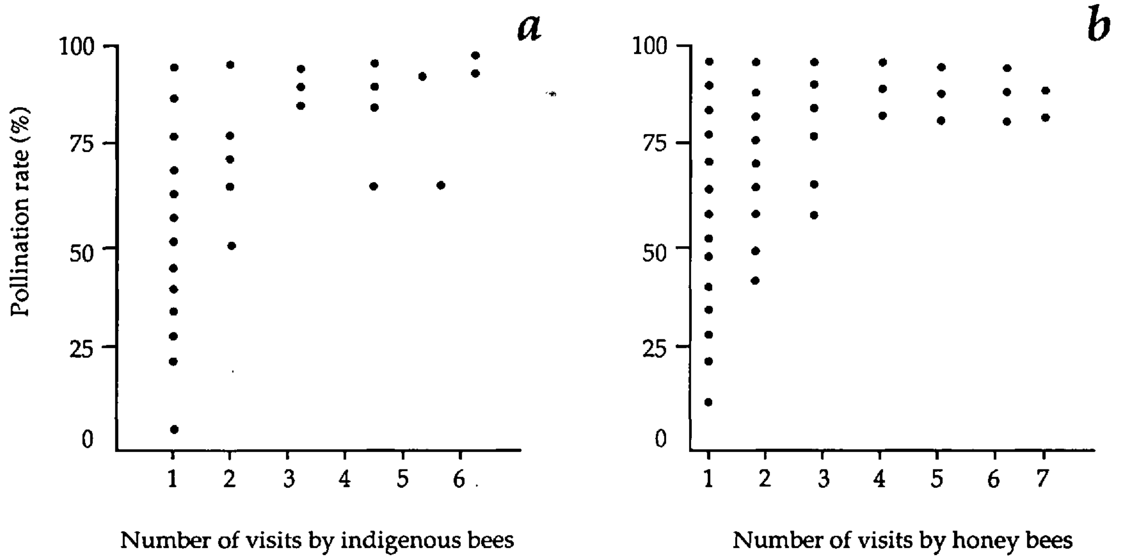

Fig. 2. Relation between the number of visits and the pollination rates. (a) Indigenous bees. (B) Honey bees.

ation in the length of first visits for these small apoids was substantial. For example, the foraging times of *Andrena nasonii* Robertson and *Dialictus lineatulus* Robertson were three times longer than those of other indigenous and honey bees (Table 1). Individuals of these species were small and rarely touched the central stigmata during their movements over the flower.

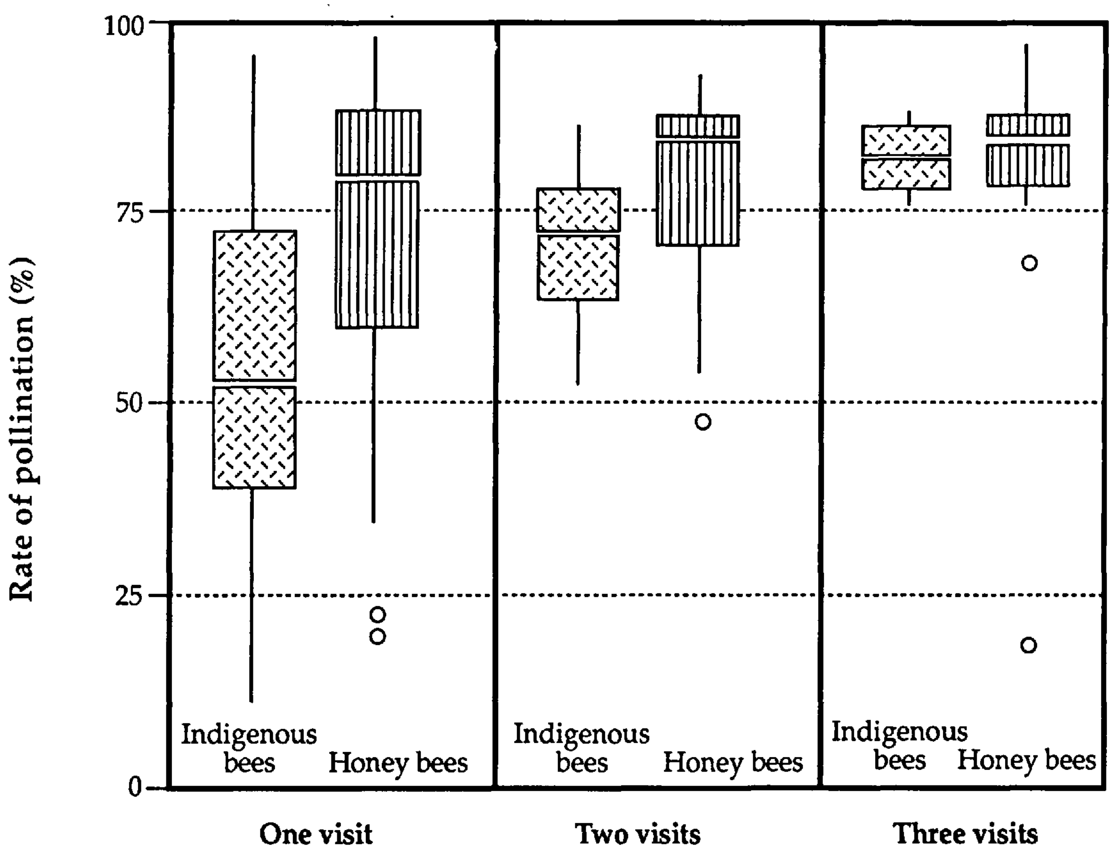

Fig. 3. Effect of number of visits of honey bees and indigenous bees on pollination rates. Each box represents 50th percentile of the most frequent values. Horizontal space in box is the median and vertical lines extend out to extremes. Separate circles indicate unusual values.

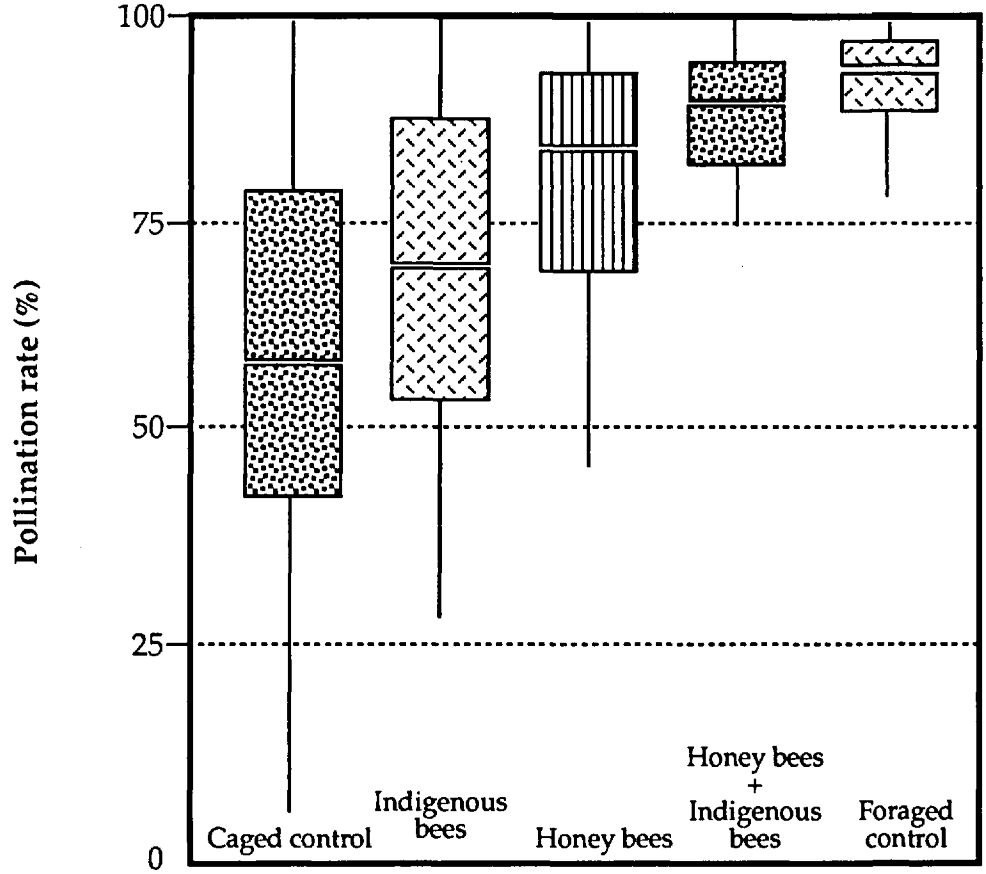

Fig. 4. Pollination rates under different pollination conditions. Each box represents 50th percentile of the most frequent values. The horizontal space in box is the median and vertical lines extend out to extremes.

Number of Visits. The correlation between the number of visits to a flower and the percentage of pollination was significant for indigenous bees ($r = 0.423$, $n = 49$, $P < 0.005$) (Fig. 2a) as well as for honey bees ($r = 0.29$, $n = 93$, $P < 0.005$) (Fig. 2b). We detected an overall difference between pollination rates of flowers having received one, two, or three visits by indigenous bees (Kruskal-Wallis test, $T = 6.45$, $n = 49$, $P < 0.05$) and honey bees (Kruskal-Wallis test, $T = 7.83$, $n = 93$, $P < 0.025$) (Fig. 3). After one visit, the pollination rate was significantly greater if flowers had been foraged by honey bees rather than by indigenous bees (Mann-Whitney U test, $Z = 3.18$, $P < 0.001$). This difference in the pollination rate between honey bees and indigenous bees was also evident after a second visit (Mann-Whitney U test, $Z = 2.15$, $P < 0.05$) but was no longer significant after the third (Mann-Whitney U test, $Z = 0.75$, $P > 0.4$). A high pollination rate (85%) may thus be obtained after three visits despite the lower efficiency of these small bees.

Complementary Effect of the Two Types of Pollinators. The following observations were made while we counted achenes: flowers foraged by indigenous bees often resulted in misshapen strawberries because of incomplete pollination in the apical region or on the side, whereas some berries resulting from visits by honey bees were poorly developed near the base. Flowers visited by both types of pollinators resulted in completely formed fruits (Fig. 4). The correlation between fertilized achenes and the weight of strawberries has already been demonstrated by Pion et al. (1984) and Chagnon et al. (1989). Based on these results, we proposed the hypothesis that strawberry development is related to the behavior of the pollinators on the flowers. To verify this hypothesis three groups of data were selected: (1) strawberries from flowers foraged by indigenous bees alone, (2) by honey bees alone, and (3) by both indigenous and honey bees. Because the number of visits influences pollination rates, data bases were sorted to select cases with equal numbers of visits for each of the three groups. These groups were then compared by pairs, as well as with the caged and the foraged controls (Table 2).

The difference between pollination percentages obtained from berries in each of the five groups was significant ($T = 73.82$, $P < 0.001$) (Fig. 4). The lowest pollination rates were found

Table 2. Comparison of the pollination rates of strawberries according to type of pollinators

Parameter[a]	Caged control	Indigenous bees	Honey bees	Honey bees and indigenous bees	Foraged control
Caged control (n = 52)		Z = 1.69 P = 0.80	Z = 2.84 P = 0.04	Z = 4.79 P = 0.000	Z = 6.03 P = 0.000
Indigenous bees (n = 35)			Z = 4.13 P = 0.000	Z = 5.68 P = 0.000	Z = 6.28 P = 0.000
Honey bees (n = 93)				Z = 2.41 P = 0.057	Z = 5.02 P = 0.000
Honey bees and indigenous bees (n = 53)					Z = 3.19 P = 0.001

[a] n, number of strawberries.
N.b. Mann-Whitney U test was used.

on the caged control berries. Pollination rates of berries resulting from flowers foraged by indigenous bees alone did not differ significantly from this control group. However, we found a highly significant difference between pollination rates of berries resulting from foraging by indigenous bees alone and by honey bees alone (Table 2). Even higher percentages were recorded for flowers visited by both pollinator types. The highest rates came from the open-field (foraged control) strawberries. This result was predictable because these berries came from flowers that had quite visibly received more visits from both types of bees.

In summary, these results highlight the complementary effect on strawberry pollination by both honey bees and indigenous bees. The former visit mainly the apical region of the receptacle, the latter the basal region and the area next to the stamens.

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