

POLLINATION OF STRAWBERRY BY THE STINGLESS BEE,  
*TRIGONA MINANGKABAU*, AND THE HONEY BEE,  
*APIS MELLIFERA*: AN EXPERIMENTAL STUDY  
OF FERTILIZATION EFFICIENCY

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SUMMARY

To know basic information about the stingless bee, *Trigona minangkabau*, and the European honey bee, *Apis mellifera*, as pollinator of strawberry, we set three greenhouse areas: the honey bee introduced area, the stingless bee introduced area and the control area. Foraging and pollination efficiencies of the two bee species were studied comparatively.

During the experimental period (10 days), the stingless bee foraged well and the nest weight did not change, though the honey bee often foraged inefficiently and the nest weight decreased by 2 kg. The average nectar volume of a flower was lower in the honey bee area (0.02  $\mu$ l) and nearly the same in the other two areas (0.1  $\mu$ l).

We make a numerical model to describe pollination and fertilization process. This model shows that one visit of the honey bee pollinated 11% of achenes and one visit of the stingless bee did 4.7% on average and that 11 visits of the honey bee or 30 visits of the stingless bee are required per flower to attain normal berry (fertilization rate, 87%). In this study, the rate of deformed berries in the stingless bee area (73%) was lower than that of the control area (90%), but higher than that of the honey bee area (51%). From our numerical model, we conclude the stingless bee could pollinate strawberry as well as the honey bee if we introduced 1.8 times of bees used in this experiment.

KEYWORDS: pollinator, strawberry, greenhouse, honey bee, stingless bee.

INTRODUCTION

Strawberry (*Fragaria chiloensis*  $\times$  *ananassa*) flowers are hermaphroditic and self-compatible to a certain extent. Berries (=fruits) are deformed at parts in which achenes are not fertilized. This berry deformity is a severe problem in commercial

cultivation of strawberries in greenhouses. The European honey bee, *Apis mellifera*, has been practically used as pollinators (Free, 1968; Abe, 1971).

However, there is a problem in use of the honey bee for pollination of strawberry; colonies frequently crash due to death of workers and low foraging efficiency in greenhouses (Katayama, 1987). Foraging range of the honey bee is up to 10 km from the hive, and the bees fly upward to a height of several dozen meters at onset of foraging (Visser and Seeley, 1982; Seeley, 1985). Due to these foraging habits, a large portion of the bees are trapped at a greenhouse ceiling to death. Moreover, pollen collection of the honey bee is not performed well on strawberry flowers. Instead of the honey bee, we began to find alternative pollinators that fit to strawberries in greenhouses and one candidate is the stingless bee, *Trigona minangkabau*.

The stingless bee, Meliponini, is a close relative to the honey bee, Apini, both in a family, Apidae. There are about 400 species of stingless bees in the tropical and subtropical regions and show high diversity of nesting and foraging habits (Schwarz, 1948; Sakagami, 1982; Roubik, 1989). In many species of stingless bees, foraging range is smaller than that of the honey bee (0.5 km) and foragers perform hovering flights near the nest entrance, not showing upward flight as honey bees. These may fit to small enclosures such as greenhouses. One possible problem is their low ability to bear cold due to their original distribution confined to tropical environments.

This study aims to get basic information about foraging activities of the stingless bee, *T. minangkabau*, on strawberries in greenhouses, in comparison with the honey bee, *A. mellifera*. The fertilization efficiency is also compared between the stingless bee and the honey bee by the experiment in which the number of bees' visits to a flower is controlled. Flowering and fruiting traits of the strawberry, e.g. nectar secretion pattern, are also clarified.

## MATERIALS AND METHODS

### Experiment Procedures

We arranged pots of a strawberry cultivar, 'Houkou-wase' (*Fragaria chiloensis* × *ananassa*), in three greenhouse areas (Fig. 1) in the campus of Shimane University, Matsue, Shimane Prefecture, Japan (E133°, N35°). One colony of the European honey bee, *Apis mellifera*, and four colonies of the stingless bee, *Trigona minangkabau*, were introduced to each of the larger two areas in which 266 pots were set. In the smaller area in which 81 pots were set, no bees were released (control area). The colony size of the honey bee was 8,000 to 10,000 bees and this size was about 25% of the average in apiculture. The stingless bee colonies were imported from Sumatra, Indonesia in March, 1988. The colony size of each of the four stingless bee colonies was 300 to 400 bees, being about 10% of matured ones (Sakagami et al., 1983; Inoue et al., 1984).

Experiments were done during the period from April 18 to 27, 1988. Weights of

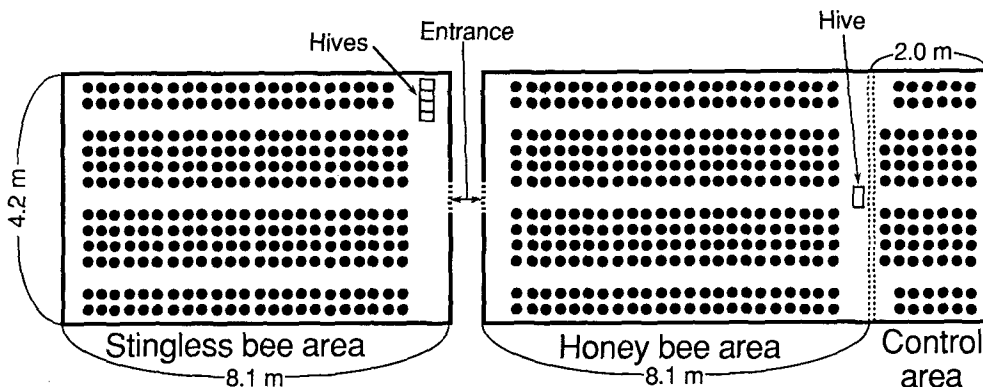


Fig. 1. Map of three greenhouse areas in the campus of Shimane University. Four hives of the stingless bee, *Trigona minangkabau*, were set in the stingless bee area, and one hive of the honey bee, *Apis mellifera*, was set in the honey bee area. No bees were released to the control area. Each ● shows a pot of strawberry.

the five hives were measured at the beginning and the end of the experiments. All flowers that bloomed before and after this period were removed. The number of flowers was counted in the honey bee and the stingless bee areas on April 21 and it was 387 and 383, respectively. Most of the flowers were secondary flowers and a few of them were thirdly. All primary flowers might bloom before the experimental periods and be removed.

Foraging activity was observed both at hive entrances and on flowers during the foraging period from 8 : 00 to 17 : 00, on April, 23, 24 and 25. At hive entrances, the numbers of bees that got out from ( $n_o$ ) and returned to hives ( $n_i$ ) were counted for 10 minutes per hour. In return flights, we distinguished pollen ( $n_p$ ), nectar ( $n_n$ ) and empty ( $n_e$ ) loads, as in Inoue et al. (1985), and  $n_i = n_p + n_n + n_e$ . To know the nectar load, we compared the abdomen size of bees retuning back with that of bees getting out by naked eyes. The numbers of bees visiting individual flowers were counted at randomly-chosen 8–15 strawberry pots for 10 minutes per hour, just the same period as observation at the hive entrances. Air temperature and luminous flux density were measured in front of hive entrances just after counts at the hive entrances.

The relationship between the number of bees' visits and the percentage of fertilized achenes was studied on 19 pots in each of the honey bee and the stingless bee areas. These pots were bagged by Tetoron mesh before and after the continuous observation period. On April 26, we took off the bags for several minutes, at most. During the unbagged period we continuously observed bees' visits and bagged again when the number of bees' visits on individual flowers reached to the planned ones (from 1 to 10).

Nectar secretion and consumption patterns were studied, by measuring the standing amount of nectar of 100 flowers at several different conditions in each area, during April 19–25. Nectar amount was measured by microcapillary tubes

(Microcap, Drummond) and sugar concentration (total dissolved solid in weight sucrose per weight solution) with a refractometer (Atago 500), individually when the amount of nectar was  $\geq 1 \mu\text{l}$ , and by pooling 2-3 flowers otherwise.

During this study, strawberry flowers were producing pollen at flower opening, and dropped the petals within a day. The life history of strawberry flowers changes by air temperature, as discussed afterward.

#### Measurement of Fertilization Rate and Berry Deformity

All berries were harvested during May 15-29, 1988. Each was weighed and checked deformity ranks. Four deformities ranked were: '−' quite few unfertilized achenes were found and not deformed, '+−' some unfertilized achenes but not deformed, '+' many unfertilized achenes and slightly deformed, and '++' very many unfertilized achenes and highly deformed. This ranking was done by naked eyes and we spent about 10 seconds per each berry at decision. Deformity caused by factors other than unfertilization was neglected in the above ranking. Twenty berries of each deformity rank from each area were sampled for further exact count of the total number of achenes and the number of fertilized achenes when the number of berries  $> 20$  and all otherwise.

#### A Model to Describe Fertilization Rate

We make a mathematical model that describes the percentage ( $P$ ) of fertilized achenes in a single berry as a function of the number ( $N$ ) of bees' visits to a flower (A strawberry flower has ca. 300 stigmata and the stigma which receive pollen grains becomes a fertilized achene). Assumptions and procedures are as follows.

(1) In self-compatible, hermaphroditic plants, some achenes are fertilized by self-pollen grains even without bees' visits. Let's  $P$  at  $N=0$  be  $P_0$ .  $P_0$  becomes 0 in self-incompatible plants.

(2)  $P$  will increase as a function of  $N$ . We assume that each visit pollinates achenes in a fixed flower area  $a$  at random and that the rate of increase of  $P$  by a single visit is the product of  $a$  and the rate of unfertilized achenes:  $dP/dN=(1-P)a$ . This assumption is according to the functional response model of prey-predator interaction (Gause, 1934; Fujii et al., 1986).

Under these two assumptions  $P$  becomes

$$P=1-(1-P_0)e^{-aN} \quad (1)$$

(3) At the population level,  $N$  can be determined by the number of bees actively foraging ( $n$ ) and the number of open flowers ( $f$ ),

$$N=\frac{b}{f} \cdot n \quad (2),$$

where  $b$  is the number of flowers visited by a single bee foraging out in unit time.

(4) Based on our observation of colony foraging activity, we estimate  $n$  as a product of the number of bees that get out from ( $n_o$ ) and return to ( $n_i$ ) the hive and the proportion of actively foraging bees, which come back with nectar or pollen.

$$n = \frac{(n_o + n_i)}{2} \cdot \frac{(n_p + n_n)}{n_i} \quad (3)$$

Statistical analysis was done by SAS package in the Data Processing Center of Kyoto University (SAS institute inc., 1985). Modified Gauss-Newton method (Hartley, 1961) was used for the non-linear regression of eq. (1).

## RESULTS

### Foraging Activity of Bees

The two estimates of foraging activity, the number of bees that get out from the hive per 10 minutes ( $n_o$ ) and the number of bees that visit on a flower per 10 minutes

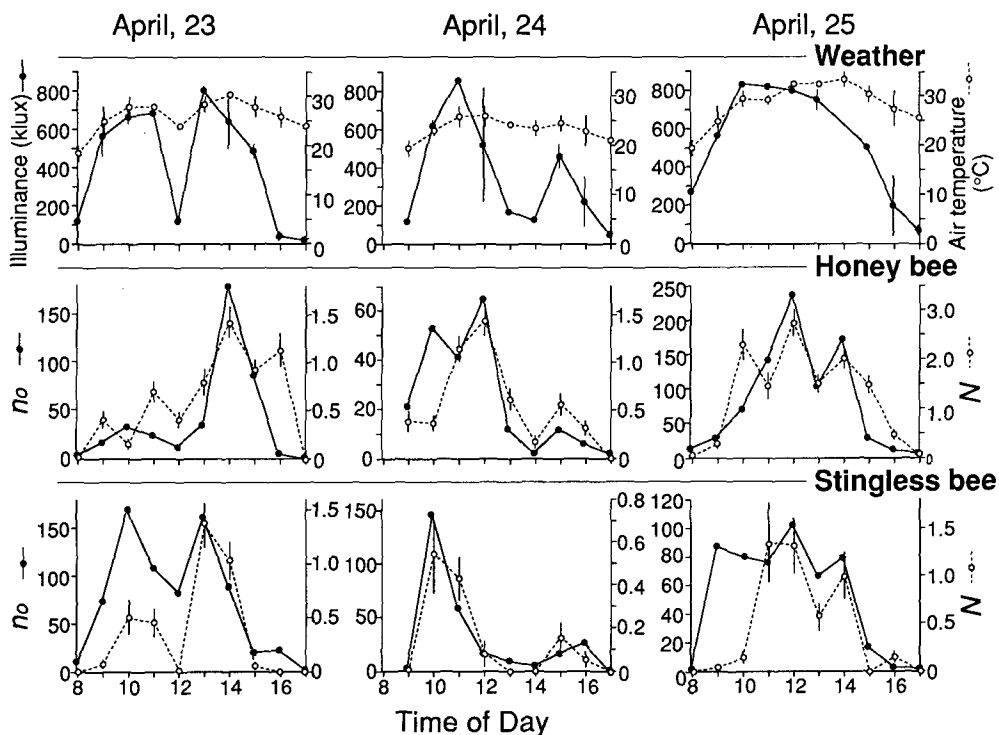


Fig. 2. Weather conditions and bee activities on April 23, 24 and 25. The upper row shows diurnal changes of weather conditions averaged over two bee introduced areas. ● shows mean value for luminous flux density (lux), and ○ shows mean value for air temperature (°C). ○ in the middle (the honey bee area) and in the bottom (the stingless bee area) rows shows diurnal changes in average number of bees visiting to a flower in 10 minutes ( $N$ ). Vertical lines show S.E. ● in the middle and in the bottom rows shows number of bees getting out from hives ( $n_o$ ).

( $N$ ) changed parallel in response to weather changes (Fig. 2). Out of returning honey bees, 53.2% carried nectar and there were very few (0.6%) pollen foragers (Fig. 3). Empty returns occupied 46.2% of the total. We observed that these bees flew just beneath greenhouse ceiling. As shown in Fig. 2, it was cloudy at the noon on April 23 and during the afternoon on April 24 and it was fine through out a day on April 25. In the stingless bee, when it was fine, percentages of pollen and nectar collection were respectively 20–30% and 50–60%. Empty returns occupied <20% of the total. At low illuminance condition, stingless bees returned without any loads, indicating that the stingless bee stopped foraging quickly in response to drop of illuminance.

The colony foraging activity,  $n$ , estimated with eq. (3), changed for different weather conditions, and the sensitivity of the changes to illumination and temperature was different between two bee species. The stingless bee was quite sensitive to changes in luminous flux density ( $p=0.0002$ ) but indifferent to changes in air temperature ( $p=0.37$ ) (Table 1). Contrarily, the honey bee was sensitive to changes in air temperature ( $p=0.05$ ) but indifferent to changes in luminous flux density ( $p=0.35$ ).

By the relationship of  $N$  and  $n$  (Fig. 4), the number of flowers visited by one honey bee foraging in 10 minutes ( $b$ ) was estimated to be 7.74 ( $=0.02 \times 387$ ). That of one stingless bee was 3.06 ( $=0.008 \times 383$ ). Mean values of  $n_o$ ,  $n$  and  $N$  were respectively 48.9 (s.e. = 11.4), 28.7 (6.7) and 0.77 (0.13) in the honey bee area and were

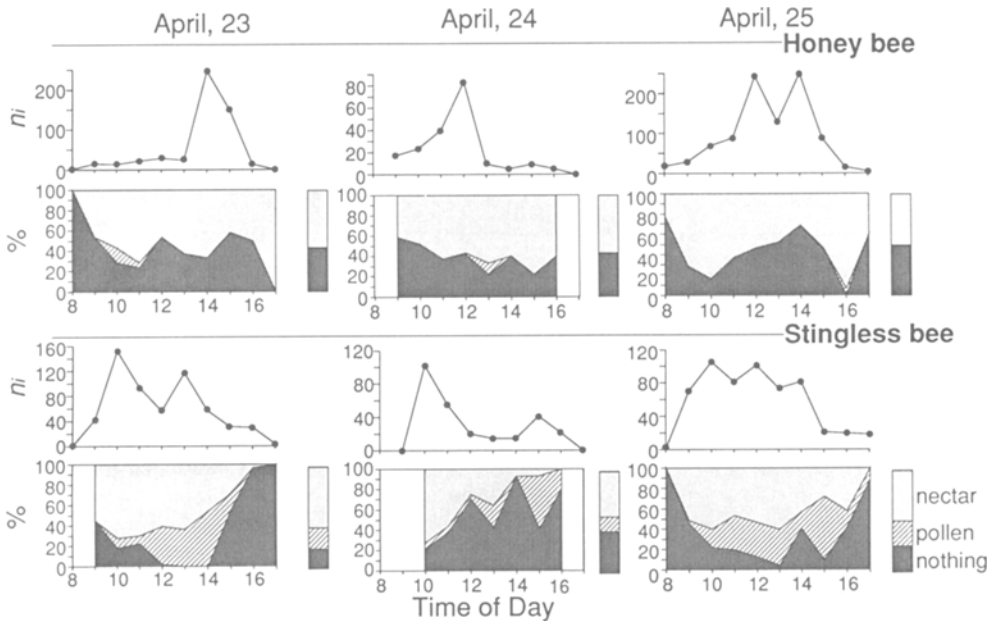


Fig. 3. Diurnal changes in the number of bees returning back to hives ( $n_i$ , shown by ●) and the percentage of bees coming back with nectar, pollen and nothing, on April 23, 24 and 25. The percentage of bees with each load over all days is shown at the right side of each graph.

Table 1. The number of bees actively foraging ( $n$ ) as a multiple linear function of air temperature (Temp) and illuminance (Lux). The model is  $n = k*(Temp) + l*(Lux) + m$

Variable (Parameter)	Parameter estimated	Standard error	t for Hypothesis: Parameter=0	P
Honey bee area				
$m$	-94.5	44.7	-2.12	0.04
$k$	4.35	2.13	2.04	0.05
$l$	0.00027	0.00029	0.93	0.35
	[ $r^2=0.51$ ]			
Stingless bee area				
$m$	-49.6	40.6	-1.22	0.23
$k$	1.51	1.65	0.91	0.37
$l$	0.00112	0.00026	4.39	0.0002
	[ $r^2=0.49$ ]			

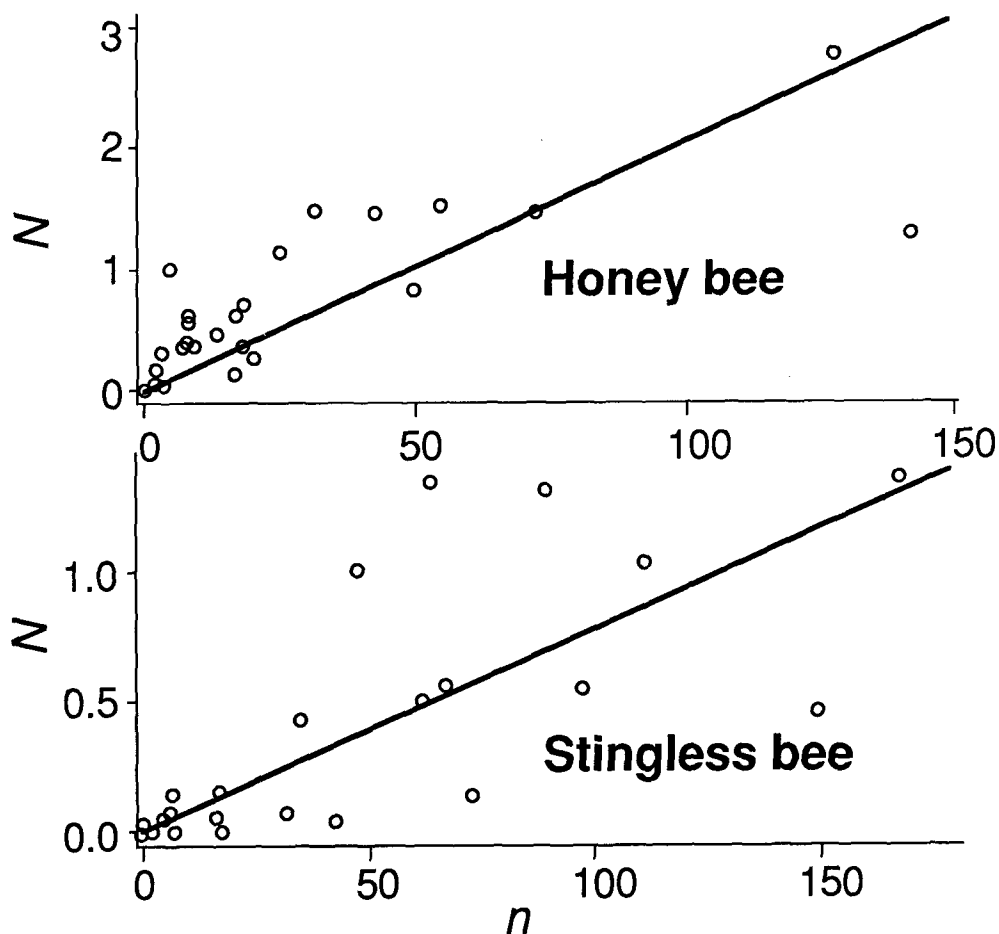


Fig. 4. The average number of bees visiting to a flower in 10 minutes ( $N$ ) as a linear function of the estimated number of active foragers ( $n$ ).  $N = (0.02 \pm 0.002)n$ , ( $r^2 = 0.76$ ) for the honey bee area and  $N = (0.008 \pm 0.0009)n$ , ( $r^2 = 0.71$ ) for the stingless bee area.

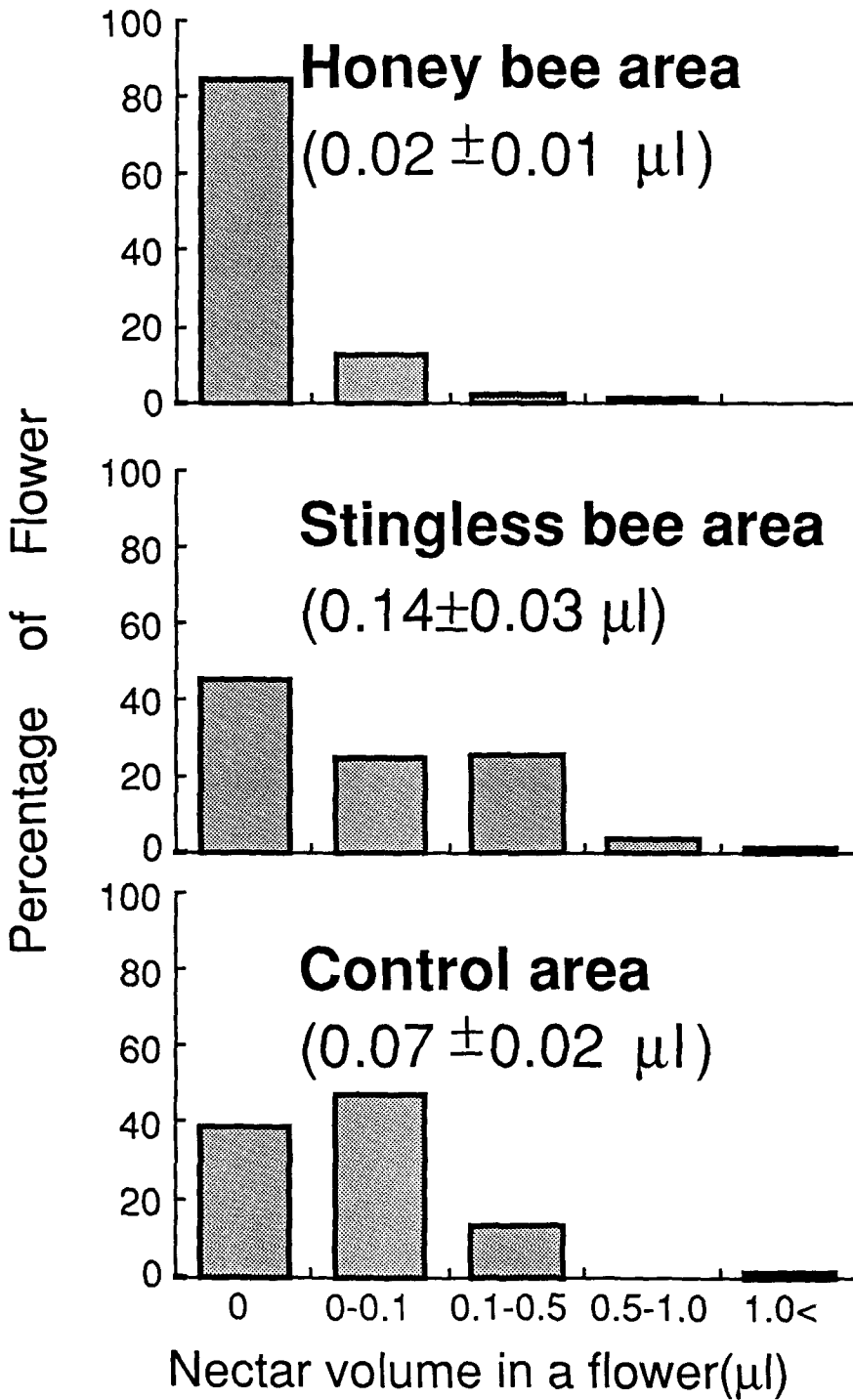


Fig. 5. Distribution patterns of nectar volume in a flower in the three areas. Values in bracket show mean  $\pm$  S.E.



respectively 52.6 (10.6), 38.2 (8.7) and 0.31 (0.08) in the stingless bee area.

The hive weight of the honey bee colony decreased by 2.3 kg during 10 days of the observation period (from 10.7 to 8.4 kg). Out of the four stingless bee colonies, one increased and three decreased in weight. The average percent decrease was  $<4\%$  (448.7 g to 451.0 g, 458.4 to 452.4, 476.3 to 475.0 and 543.4 to 536.0, the weight of the hive wood box = 330 g). These changes of hive weight reflected the difference of foraging activities between the two species, as shown above.

#### Nectar Secretion and Consumption

The average nectar volume of an unbagged flower was  $0.02 \mu\text{l}$  in the honey bee,  $0.14 \mu\text{l}$  in the stingless bee and  $0.07 \mu\text{l}$  in the control areas (Fig. 5). Nectar of flowers in the honey bee area was consumed significantly in comparison with the control area (Welch-Aspin's  $t=2.2$ ,  $p=0.03$ ). More than 80% flowers in the honey bee area did not have any measurable nectar. There was no significant difference of nectar volume between the stingless bee and the control area (Welch-Aspin's  $t=1.9$ ,  $p=0.06$ ).

Nectar volume of a flower significantly varied only by the effect of the area (ANOVA,  $F=5.36$ ,  $p=0.006$ ), but not by the effects of sampling date ( $F=0.54$ ,  $p=0.78$ ), time of day ( $F=1.35$ ,  $p=0.20$ ) and the interactions of these three factors ( $F=1.87$ ,  $p=0.57$  for area  $\times$  date,  $F=0.47$ ,  $p=0.95$  for area  $\times$  time, and  $F=0.48$ ,

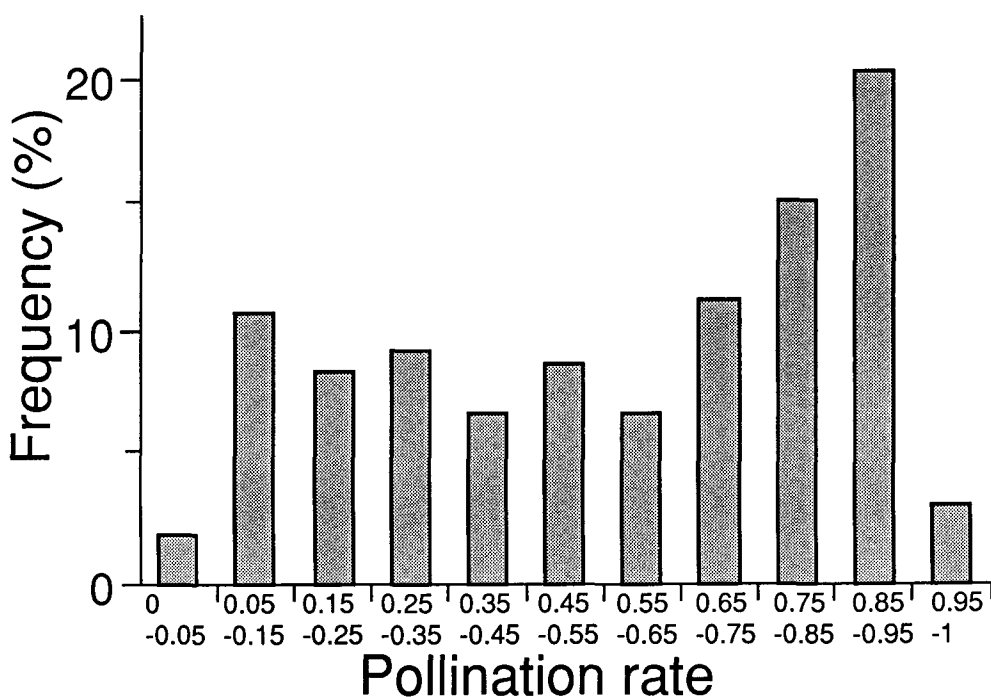


Fig. 6. Frequency distribution of fertilization rate when no pollinator visits ( $P_0$ ). See the text for details.

$p=0.93$  for date  $\times$  time).

Sugar concentration was 30–40% ( $m=35.5$ ,  $S.E.=5.1$ ,  $n=137$ ), and did not differ by date, time of day or area.

### Fertilization Pattern

Frequency distribution of the percentage of fertilized achenes ( $P$ ) of 364 berries in bagged flowers that did not received any bee's visit had large variance ( $CV = 51.2\%$ ) with the average of 56%, and there were two peaks at both edges (Fig. 6). It did not fit to normal distribution ( $D\text{-normal}=0.12$ ,  $p<0.01$ ) nor uniform distribution ( $\chi^2=64.1$ ,  $p<0.01$ ).

The relationship between the percentage of fertilized achenes ( $P$ ) and the number of bees that visited to a flower ( $N$ ) was well fit to eq. (1) in both the honey bee and the stingless bee areas (Fig. 7).  $P_0$  estimated by eq. (1) was 0.557 ( $S.E.=0.023$ ) in the honey bee area and was 0.459 ( $S.E.=0.026$ ) in the stingless bee area. Both values were not significantly different from the mean value of direct observation, 56%

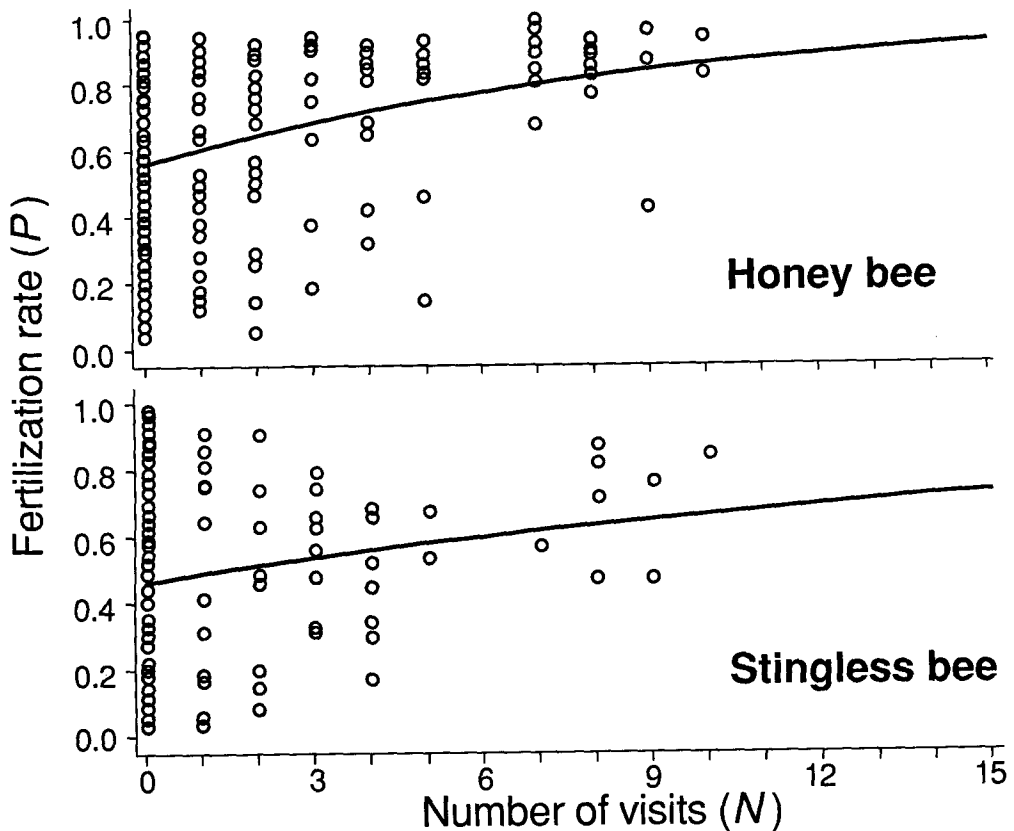


Fig. 7. Fertilization rate ( $P$ ) as a function of the number of bee visits ( $N$ ).

$P=1-(1-0.56)e^{-0.11N}$  for the honey bee area and  $P=1-(1-0.46)e^{-0.047N}$  for the stingless bee area.

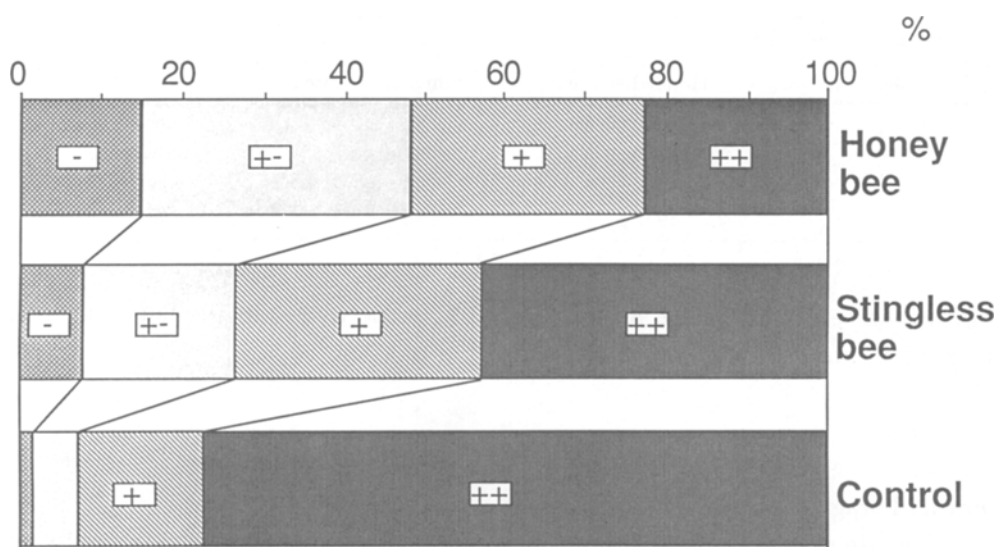


Fig. 8. Percentages of harvested berries in each deformity ranks ('-': no unfertilized achenes, '+-': some unfertilized but not deformed, '+': slight deformities, '++': heavy deformities) from unbagged plants in the three areas.

( $p > 0.05$ ).  $a$  was 0.11 (s.e. = 0.03) in the honey bee area and was 0.047 (s.e. = 0.027) in the stingless bee area, implying that one honey bee's visit pollinated 11% of achenes and one stingless bee's visit did 4.7%.

#### Harvested Berry Data

The number of harvested berries was 1772, 1561 and 497 in the honey bee, the stingless bee and the control areas respectively. The average weights of a berry was 6.56, 6.24 and 5.57 g respectively. More than 90% of berries harvested from the control area was deformed (Fig. 8, Table 2). The percentage of deformity was respectively 51 and 73% in the honey bee and the stingless bee areas.

Berries at higher deformity ranks were lighter, except for '-' rank in the control area that had few samples (Table 2). The percentage of fertilized achenes ( $P$ ) also decreased in increase of deformity rank (Table 3).  $P$  at '+' rank was higher in the honey bee area than in the other two areas due to unknown reason. Based on Table 3 and percentages of ranks in each area (Fig. 8), the average percentage of fertilized

Table 2. Weight (g) of a berry at each deformity rank in the three areas, shown by mean  $\pm$  S.E. (the number of harvested berries).

Deformity rank	Honey bee area	Stingless bee area	Control area
-	9.7 $\pm$ 0.3 (261)	9.7 $\pm$ 0.5 (117)	7.5 $\pm$ 0.9 (6)
+ -	7.3 $\pm$ 0.1 (603)	8.2 $\pm$ 0.2 (305)	10.6 $\pm$ 1.1 (31)
+	6.0 $\pm$ 0.1 (520)	6.4 $\pm$ 0.1 (464)	7.5 $\pm$ 0.5 (76)
++	4.1 $\pm$ 0.1 (388)	4.6 $\pm$ 0.1 (675)	4.8 $\pm$ 0.2 (384)

Table 3. The percentages of fertilized achenes per berry at each deformity rank, in the three areas, shown by mean  $\pm$  S.E.

Deformity rank	Honey bee area	Stingless bee area	Control area
—	91.8 $\pm$ 0.5	91.2 $\pm$ 0.6	90.7 $\pm$ 0.8
+ —	87.7 $\pm$ 0.7	87.4 $\pm$ 0.7	84.1 $\pm$ 0.9
+	81.3 $\pm$ 1.0	76.5 $\pm$ 1.2	74.7 $\pm$ 1.3
++	69.6 $\pm$ 1.9	56.2 $\pm$ 3.4	55.2 $\pm$ 2.9

achenes was estimated to be 81, 70 and 62%, respectively, in the honey bee, the stingless bee and the control areas.

## DISCUSSION

### Diurnal Foraging Activity

The stingless bee, *Trigona minangkabau*, is active in foraging almost uniformly throughout a daytime (7 : 00–18 : 00) at fine weather conditions in the original distribution area, Sumatra (Inoue et al., 1985). The stingless bee used in this study was imported from there to Matsue, Japan. In the greenhouse in Matsue, foraging activity of the stingless bee was limited into the period from 9 : 00 to 14 : 00 even at fine weather conditions. Air temperature is not responsible for this limitation because, until 17 : 00, it was higher than the lower limit for foraging in Sumatra, 24°C. In Sumatra, bees start foraging at 7 : 00 when air temperature is 24°C and continue until sunset, 18 : 00 (27°C). Day length in April in Matsue is rather similar to Sumatra. Resource consumption is also not the limiting factor of diurnal activity because much nectar and pollens remained until sunset in the experiment. Thus, we cannot explain the reason of this limitation by these factors.

The stingless bee was quite sensitive to changes in luminous flux density. It is especially significant and quick when dark cloud passed over the greenhouse during 9 : 00 to 14 : 00. Possible adaptive significance of this high sensitivity is discussed below.

In the tropical South-East Asia, rain starts usually in the late afternoon but occasionally in the morning. Rain is quite strong, often accompanied with squall and many bees at foraging die at this time. The average life span after start of foraging was about 5 days in Sumatra (Inoue, unpub.) but it was 20 to 30 days in the greenhouse in Matsue in which there was no such adverse conditions (Tezuka, et al., unpub). Before start of rain, dark cloud covers sky and, thus, drop of luminous flux density (or factors related to this) is a good sign to predict rain. At this dark condition, many bees return to the nest before rain, although many bees fails to do so at the same time. Bees in the nest stop departure at dark conditions. Thus the quick response to drop of luminous flux density must be quite adaptive to reduce the major mortality cause and it did not change even in the greenhouse in which there was no possibility of rain. The same behavior is also found in the tropical bumble bee, *Bombus rufipes*, in

Sumatra (Kato et al., unpub).

On the other hand, the honey bee was not sensitive to changes in luminous flux density and, instead, they were sensitive to changes in air temperature. This is thought to be adaptive in the temperate regions because, especially in early spring, cost of thermoregulation during foraging increases in low air temperature and it often links to death due to loss of body temperature. In spring, cold weather often appears under high atmospheric pressure and it does not accompany rain.

Even in the experimental conditions in the greenhouse, both the stingless bee and the honey bee are thought to control their foraging, based on signs that used in their original environments.

In Sumatra, the stingless bee, *T. minangkabau*, forages pollens mainly in the morning (7 : 00–10 : 00) and this is common to other stingless bees in tropical regions (Inoue, et al., 1985; Roubik, 1989). In this experiment, the stingless bee collected pollens more frequently in the afternoon. We could not explain this shift. The honey bee very rarely collected pollens in the experiment. Shortage of honey stock was indicated by the decrease of the hive weight (2 kg) and this might force honey bees to concentrate their effort to nectar collection.

The average nectar volume of a flower in each area also shows shortage of nectar for the honey bee. There was no significant difference of nectar volume between the stingless bee and the control areas (Fig. 5). This means that the strawberry flower secreted nectar compensatorily to some extent. But, the nectar volume in the honey bee area was significantly lower than the other two areas. This means that consumption by the honey bee was much more than compensatory nectar secretion of the strawberry flower.

#### Flowering Phenology and Fertilization

Each strawberry produced on average 1.5 flowers per day during the experimental period, and in total 400 flowers daily opened in both the stingless bee and the honey bee areas. Each flower opened for at most one day in this experiment. The fertilizable period (the period during which a stigma is ready for fertilization) is thought to be shorter than one day as shown below. At the lower air temperature, life span of strawberry flowers is the longer. In greenhouses commercially cultivated during winter, longevity of the flower is more than a week (reviewed by Abe, 1971). In our experimental greenhouse at early April, 1990, the flower drops petals at three days after flower opening (Maeta et al., 1992), and can fertilize for about a week (Maeta et al., unpub.). We should know the life span of the flower in this experiment was very short because of high temperature.

Self-compatibility or the percentage of fertilized achenes in bagged flower ( $P_0$ ) was highly variable among flowers. Such a high variability was also observed in another cultivar of strawberry (Chagon et al., 1989). They found that  $P_0$  of primary flowers was lower than secondary and following flowers. But, this factor cannot

explain our result because our experimental period was short (10 days) and most flowers were secondary.

On average 11% of achenes were fertilized by one visit of the honey bee and it was 4.7% in the stingless bee. Difference of body surface area (1 : 0.33) is one factor responsible for difference of fertilization efficiency between bee species (11 : 4.7 = 1 : 0.43). Another factor is behavior of bees on flowers (See Maeta et al., 1992).

In the honey bee area, average fertilization rate of unbagged flower was 0.81 (Table 4). The number of visits to attain this value is estimated to be 8 based on eq. (1) of which parameters were obtained by the bagging experiments. However, direct observation on open flowers showed the actual number of visits was 46.2/day for the average. Thus, if eq. (1) well describes actual fertilization process and the fertilizable periods is one day, the fertilization rate should be higher. This discrepancy may be due to lower fertilization efficiency of the honey bee and/or shorter fertilizable period of a flower. At present we could not detect which is more important.

In the stingless bee area, average fertilization rate of unbagged flowers was 0.70 (Table 4). To attain this value, eq. (1) estimates the number of visits per flower to be 13, but it was actually 18.6/day on average. Compared with honey bees the difference between the two values is small. But still the estimated value by eq. (1) was small under assumption that the fertilizable period is one day. Below we tentatively use values based on eq. (1).

Commercial market requires production of strawberries of which the deformity rank is '–' or '+–'. The average fertilization rate ( $P$ ) at '+–' was about 0.87 (Table 3). We call this  $P$  'economic threshold for a berry'. To realize this threshold, 11 visits are required per flower when we use the honey bee, and 30 visits are required when we use the stingless bee (From eq. (1), Table 4). Number of the honey bee visits to realize this threshold was estimated higher, 16 to 19, by Skrebtsova (1957) and lower, 4, by Chagnon et al. (1989). These differences may occur mainly because of the difference of strawberry cultivars used in each study.

The economic threshold for a berry, discussed above, is one thing, and economic threshold for a greenhouse is another. In the honey bee area, estimated  $N$  to attain the

Table 4. Estimated variables for activity of bees and pollination.

Variables	Honey bee area	Stingless bee area
No. of going-out bees: $n_o$	48.9/10 min 2934/day	52.6/10 min 3156/day
No. of foraging bees: $n$	28.7/10 min 1722/day	38.2/10 min 2292/day
No. of visits per flower: $N$	0.77/10 min 46.2/day	0.31/10 min 18.6/day
No. of total flowers: $f$	387/house	383/house
No. of flowers visited by a bee: $b$	7.74/10 min	3.06/10 min
Average fertilization rate: $\bar{P}$	0.81	0.70
Estimated $N$ to attain $\bar{P}$	8	13
Economic threshold of $N$	11	30

actual average fertilization rate was 8. So that, under above assumptions, a honey bee colony with 1.4 times (11/8) workers may provide 11 visits for a flower and make a normal berry on average. But, this does not mean that the colony with 1.4 times workers fit to our experimental house for commercial use.

In commercial production of strawberries in greenhouses, longevity of the flower is more than one week because of low temperature (Abe, 1971) and some berries are thinned out so as to make large good berries. In this experiment, the fertilizable period may be less than one day and we harvested all berries from the flowers during the 10-day experimental period. Because of these reasons, the rate of deformed fruits is so high (51%) for economical use even in the honey bee area, though it is <1% in an actual commercial greenhouse of lower temperature using one colony of the honey bee for pollinator (Abe, 1971). The result in this study does not mean more than one honey bee colony should be introduced into a greenhouse.

Since the stingless bee was less sensitive to changes in air temperature than the honey bee in this study, we may safely presume that the stingless bee colony size which attain the same fertilization rate as the honey bee area could fit to commercial use like the honey bee. The actual fertilization rate in the honey bee area was 81% on average. To attain this rate by the stingless bee, eq. (1) estimates the number of visits per flower to be 24. This value is 1.8 times as estimated  $N$  from fertilization rate in the stingless bee area (Table 4). Thus, we conclude that the stingless bee colony with 1.8 times worker (=3,000 workers=two mature colonies or 8 small colonies used in this experiment) may pollinate strawberry as well as one colony of the honey bee used in a commercial greenhouse.

ACKNOWLEDGMENTS: We thank R. Miyanaga, T. Hasegawa, K. Saitou, T. Okamoto, T. Ohtsubo and K. Koyanagi of Shimane University for their kind collaboration to get data. This study was partly supported by a grant from Sumitomo Chemical Co. The analysis of this study was partly supported by a Grant-in-Aid for JSPS fellowships from the Japanese Ministry of Education, Science and Culture to T. K. (No. 0950).

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ミナンカバウハリナシバチとセイヨウミツバチによるイチゴの送粉：  
受精効果に関する実験的研究

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ミナンカバウハリナシバチ *Trigona minangkabau* とセイヨウミツバチ *Apis mellifera* の、イチゴハウスでの送粉者としての基本的特性を知るため、ハリナシバチ放飼ハウス、ミツバチ放飼ハウス、および無放飼ハウスの3区を設けて、2種のハチの採餌行動と送粉効率を比較した。

10日間の放飼期間中、ハリナシバチは効率よく採餌し、巣の重量がほとんど低下しなかったが、ミツバチはしばしば非効率な採餌飛行を行い、巣の重量が約2kgも低下した。花当りの花蜜量はミツバチ放飼ハウスで低く(0.02  $\mu$ l)、ハリナシバチ放飼ハウスと無放飼ハウスではほとんど差がなかった(約0.1  $\mu$ l)。

送粉受精過程の数理モデル化により、ミツバチは1回の訪花で、平均的には11%の雌しべに送粉できるのに対して、ハリナシバチは4.7%にしか送粉できないことが明らかになった。さらに、このモデルから正常巣(受精率87%以上)を生産するためには、ミツバチでは11回の訪花が、ハリナシバチでは30回の訪花が必要と推定された。今回の実験では、ハリナシバチ放飼ハウスの奇形果率(73%)は、無放飼ハウス(90%)よりは低く、ミツバチ放飼ハウス(51%)よりは高かった。しかし、先のモデルから今回用いたハリナシバチの働きバチ数の1.8倍のハチを放飼すれば、ミツバチと同様の奇形果率にできると結論された。