

FORAGING BEHAVIOR OF INDIVIDUAL WORKERS AND FORAGING DYNAMICS OF COLONIES OF THREE SUMATRAN STINGLESS BEES^{1,2)}

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INTRODUCTION

The two groups of highly eusocial bees, honeybees (*Apis*) and stingless bees (Meliponini) are both rich in pollinator assemblages of Southeast Asia. About 50 species of stingless bees are recorded (SAKAGAMI, 1982) and 6 species of honeybees (MAA, 1953; SAKAGAMI et al., 1982). Twenty two stingless bee and three honeybee species have been found in Sumatera Barat, at the site of this study. Here, 5 stingless bee species and all the honeybee species inhabit continuously-disturbed areas such as orchards and villages and the remaining stingless bees are found mainly in primary rain forests. In both areas stingless bees are major visitors of various flowering plants.

Foraging behavior of stingless bees has been mainly studied in Central and South America: LINDAUER and KERR (1958, 1960), KERR and ESCH (1965) and the other works which are reviewed by MICHENER (1974) studied their resource communication behavior, and JOHNSON and HUBBELL (1974, 1975), HUBBELL and JOHNSON (1977, 1978), ROUBIK (1978, 1979, 1980, 1981, 1982), ROUBIK and ALUJA (1983) and ROUBIK and BUCHMANN (1984) observed patterns of interspecific resource partitioning. However, no observation of stingless bees' foraging behavior has been made in Southeast Asia (but see KOENIGER and VORWOHL, 1979 in Sri Lanka).

In most of the above studies, the patterns of foragers' visits and changes in standing crops of floral resources were observed mainly on flowers or feeders. These approaches are convenient to observe direct interactions on floral resources. In this study, however, observations are made mainly at nest entrances, by counting the number of foragers which go out from and come back to a nest, and measuring the amount of resources brought back per foraging flight and the foraging durations of individual foragers. By these observations, the foraging behavior of individual workers and foraging dynamics of entire colonies is clarified in three Sumatran stingless bees which live in disturbed areas. At the same time, the intensity of competition against floral resources is indirectly assessed.

¹⁾ Contribution to the ecological and bioeconomical studies of the stingless bees. 4.

²⁾ Contribution No. 17 of Sumatra Nature Study (Entomology).

MATERIALS and METHODS

Stingless Bees

Out of 22 stingless bee species collected so far in Sumatera Barat, *Trigona* (*Tetragonula*) *minangkabau* SAKAGAMI and INOUE is the most common in disturbed areas. This small bee (worker's wing length=3.81 mm) has moderate colony size (maximum number of workers=2600), high acceptance of human constructs as nest sites and low aggressiveness (SAKAGAMI et al., 1983; INOUE et al., 1984; SAKAGAMI and INOUE, 1985). After stopping intranidal tasks, workers about 20 day-old start foraging. Median life span of workers is about 40 days and the maximum 150.

Trigona (*Heterotrigona*) *itama* COKERELL is most abundant in secondary forests, and is of medium body size (6.15 mm), moderately large colony size (>5000) and aggressive guard bees at the nest.

Trigona (*Trigonella*) *moorei* SCHWARZ nests in aerial ant nests (*Crematogaster* sp), is also abundant in secondary forests, and is of medium body size (4.60 mm), moderate colony size (several thousands) and low aggressiveness.

Study Area

Observations were mainly undertaken at the Laboratory of Sumatra Nature Study (SNS) in the suburbs of Padang, Sumatera Barat (0°57'S 100°20'E 150 m alt.). The SNS Laboratory is surrounded by villages, orchards of tropical fruit trees (e.g. rambutan and mango), palm trees and gardens of ornamental plants. Some observations were done at the Guest House of Andalas University in the city area of Padang (see SAKAGAMI et al., 1983 for the location), where also palm trees and ornamental plants are planted.

In this area there is no defined dry season; monthly precipitation is about 500 mm in the wettest season (October–December) but even in the other months is near 300 mm, with an annual total of 4200 mm. Observations were performed in January and February, 1982, after the season of heavy rains.

Diurnal Changes in Foraging Activity

Four colonies of *T. minangkabau* (Tm_1 , Tm_2 , Tm_3 and Tm_4), one of *T. moorei* and one of *T. itama* were placed in observation hives. Tm_1 was a mature colony (No. of workers>2000) and had entered the phase of reproductive swarming (Inoue et al., 1984). Both Tm_3 and Tm_4 were medium size colonies (≈ 1000) and were rapidly increasing the worker population. Tm_2 was a small colony several months after swarming (≈ 100) with few brood. *T. moorei* was a mature colony (>2000 workers) and had begun reproductive activity (queen production). *T. itama* had already recovered from the damage due to the transfer on December 26, 1981 and had about 4000 workers.

Censuses were done on January 18, 19, 22 and 23. From about 1 m of the entrance, we counted, for 10 min per hour, the numbers of workers which went out and came back. The numbers of flights per hour were then calculated by multiplying the observed counts

Table 1. Codes of foraging and some other behavior of stingless bees' workers.

Code	Meanings
<i>T</i>	Dumping of trash
<i>E</i>	Exercise flight mainly by inexperienced workers
<i>P</i> , <i>P</i> ⁺ , <i>P</i> ⁺⁺	Collection of pollen. When possible, the amount of pollen is distinguished by <i>P</i> ⁺ (distinct load) and <i>P</i> ⁺⁺ (full load)
<i>R</i> , <i>R</i> ⁺ , <i>R</i> ⁺⁺	Collection of resin
<i>N</i> ⁺ , <i>N</i> ⁺⁺	Collection of nectar
<i>N</i> ⁻	Unsuccessful foraging flight
<i>N</i>	<i>N</i> ⁺ , <i>N</i> ⁺⁺ and <i>N</i> ⁻
<i>O</i>	Departures for foraging
<i>I</i>	Returns from foraging
<i>S</i>	Staying in nest for handling collected resources or for resting

by 6. The flight or foraging behavior of workers were classified into one of 7 categories (Table 1): A worker that dumps trash goes out holding a ball of trash in her mandibles and comes back after short flight, 1–2 m distant from the entrance (henceforth referred to as *T*). Some, mainly inexperienced workers continuously and slowly fly within a radius of about 2 m from the entrance. We call this “exercise” flight (*E*). We regard departures from the entrance other than *T* and *E* as foraging flights (*O*). Three kinds of resources are collected by stingless bees. Pollen (*P*) and plant resin (*R*) are carried on the corbiculae of the hind legs. These are distinguishable by differences of shape and color. We recognized nectar foragers by their swollen, transparent metasomas and their slow entrance into the nest (*N*⁺). We define returns other than *P*, *R* and *N*⁺ as unsuccessful foraging flights (*N*⁻). *N* is used when *N*⁺ and *N*⁻ are not distinguished from each other.

Amounts of Nectar and Pollen Loads

A forager coming back with a nectar load was captured with an insect net in front of the entrance and killed in a bottle with hydrocyanic acid. To measure nectar volume (V_n), we applied a microcapillary tube to proboscis, and squeezed the bee, whereupon it regurgitated nectar. Sugar concentration (s , total dissolved solids in weight sucrose per weight solution) was measured by refractometer (Atago 500). Sugar weight (W_s) was calculated by the equation, $W_s = sg V_n / (s + g - sg)$, where g is the specific gravity of sucrose (=1.552).

Pollen loads on both corbiculae of a forager were classified into three grades in size: large (*L*), medium (*M*) and small (*S*). The size of each pollen load was measured: the diameter of load along corbicula (l_1), that at the right angle to l_1 (l_2), and the height of load (h). Regarding each pollen load as an elliptical cone, we calculated the volume of load (v_1) by the equation, $v_1 = \pi l_1 l_2 h / 12$. Another way to estimate the volume of a pollen load is as follows. The number (n) of pollen grains per load was counted by Thoma blood count plate and the diameter (l_3) of each pollen grains was measured

under microscope. Then the estimated volume (v_2) is given by $v_2 = \pi l_3^3 n / 6$.

Censuses were done on February 18 and 19 for *T. minangkabau* and *T. moorei* and on January 22 and 23 for *T. itama* at the SNS Laboratory, and on January 11 and 14 again for *T. minangkabau* at the Guest House. Diurnal changes in amounts of loads were analyzed by dividing daytime into 5 periods (0700–1000, 1000–1200, 1200–1400, 1400–1600 and 1600–1800). Local time, =GMT+0700, is used in this paper.

Flight Sequences of Individual Foragers

On February 10, paint marks were placed on the mesoscutum of about 50 foragers in *Tm*₄. Out of these, 27 foragers were observed, at least once, to go out from the nest during the observation period from February 11 to 14. On February 11 we started continuous observations, using a tape recorder, from 0802 but foraging activity stopped at 1100 due to rain. On February 12 the observation was confined to 0910–0953 also due to rain and 0810–1400 on February 13 due to strong wind and squalls. On February 14 we made observations throughout the day (0710–1820). Such interruption of foraging activity by rains is a frequent event even after the wettest season of the tropical rain forest zone in Southeast Asia.

Before the morning of February 13 we distinguished 5 kinds of returns, *P*, *R*, *N*⁺, *N*⁻ and *E*. From the afternoon we further divided *P* into *P*⁺⁺, fully pollen laden, and *P*⁺, distinctly pollen laden, *R* into *R*⁺⁺ and *R*⁺, *N*⁺ into *N*⁺⁺ and *N*⁺. Some foragers brought back two kinds of resources at the same time. In such a case, we denoted, for example, *N*⁺⁺*P*.

RESULTS

Diurnal Changes in Foraging Activity

The daily total numbers of flights per colony are shown in Table 2. In almost every case the number of departures (*O*) was smaller than that of returns ($I = N + P + R$), due to the higher risk of overlook of departures, in which foragers soon disappear from sight, than of returns, in which foragers can be followed even after entering the entrance made by transparent tube.

The mean daily total number of returns (*I*) of *T. itama* was largest among 6 colonies (about 7000). Those of *T. moorei* and *Tm*₁ of *T. minangkabau* were about 2400, and *Tm*₃ and *Tm*₄ about 1200. *Tm*₂ was inactive. These differences may essentially reflect the different numbers of adult bees among these colonies.

Percentages of full nectar loads (*N*⁺) in total returns without pollen and resin (*N*) were nearly 80% or more in all the 3 species. Hence, subsequently all *N* were assumed to represent nectar loads. The mean percentage of nectar loads in total returns ($100 N/I$) was about 77% in *T. minangkabau*, 71% in *T. moorei* and 85% in *T. itama*. The mean percentage of pollen loads ranged 10–20% (17% in *T. minangkabau*, 20% in *T. moorei* and 12% in *T. itama*) and that of resin loads was lower than 10%.

Table 2. Daily total numbers of departures (O), returns ($I=N+P+R$), pollen (P), resin (R) loads of stingless bees, *Trigona* (*Tetragonula*) *minangkabau* (Tm_1 – Tm_4), *T. (Trigonella) moorei* and *T. (Heterotrigona) itama*. Percentages of full nectar loads (N^+) in $N(=I-P-R)$ were censused in the first 2 days. Flights for trash dumping flights (T) and exercise flights (E) were separately counted from O and I .

Colony	Date	O	I	N	$N^+\%$	P	R	T	E
<i>Trigona</i>	18	2407	2764	2339	96	276	149	174	6
<i>minangkabau</i>	19	1978	2244	1715	93	316	213	192	0
Tm_1	22	2097	2470	1845	—	487	138	227	12
	23	1858	2227	1496	—	517	214	101	0
	m	2085	2426	1847	—	399	179	174	5
Tm_2	18	139	187	181	97	6	0	6	0
	19	114	114	96	88	18	0	18	0
	22	305	318	240	—	72	6	30	0
	23	149	222	132	—	66	24	0	0
	m	177	210	162	—	41	8	14	0
Tm_3	18	967	1263	1042	75	203	18	150	0
	19	687	1192	935	78	251	6	192	0
	22	854	1141	746	—	209	186	72	6
	23	931	1093	714	—	137	242	100	0
	m	860	1172	859	—	200	113	129	2
Tm_4	18	788	944	654	79	191	99	228	0
	19	971	1057	818	83	173	66	204	0
	22	1149	1463	1277	—	162	24	192	12
	23	1180	1445	1137	—	237	71	208	0
	m	1022	1227	972	—	191	65	209	3
<i>T. moorei</i>	18	2990	3567	2620	89	624	323	385	30
	19	1452	1965	1206	86	401	358	222	34
	22	1705	1888	1445	—	372	71	72	12
	23	1675	1919	1360	—	469	90	84	0
	m	1956	2335	1658	—	467	211	191	19
<i>T. itama</i>	18	5960	6167	4449	93	1581	137	420	18
	19	4877	4942	3527	96	1265	150	295	0
	22	8407	8816	8297	—	273	246	275	96
	23	7832	8094	7484	—	352	258	326	6
	m	6769	7005	5939	—	868	198	329	30

The exercise flights (E) were more frequent in active colonies (e.g. *T. itama*, *T. moorei* and Tm_1) than in inactive ones (e.g. Tm_2), probably due to the difference in recruitment of young foragers.

The first forager went out from the entrance at around 0645 soon after sunrise (6030) and the number of foraging flights increased almost linearly until 1000 to a plateau. In the fine weather foraging continued until sunset (1830) and some workers came back in the dusk.

Figure 1 shows diurnal changes in foraging activities on January 18 and 19. Henceforth the inactive colony Tm_2 is excluded from analysis. On January 18 the number of

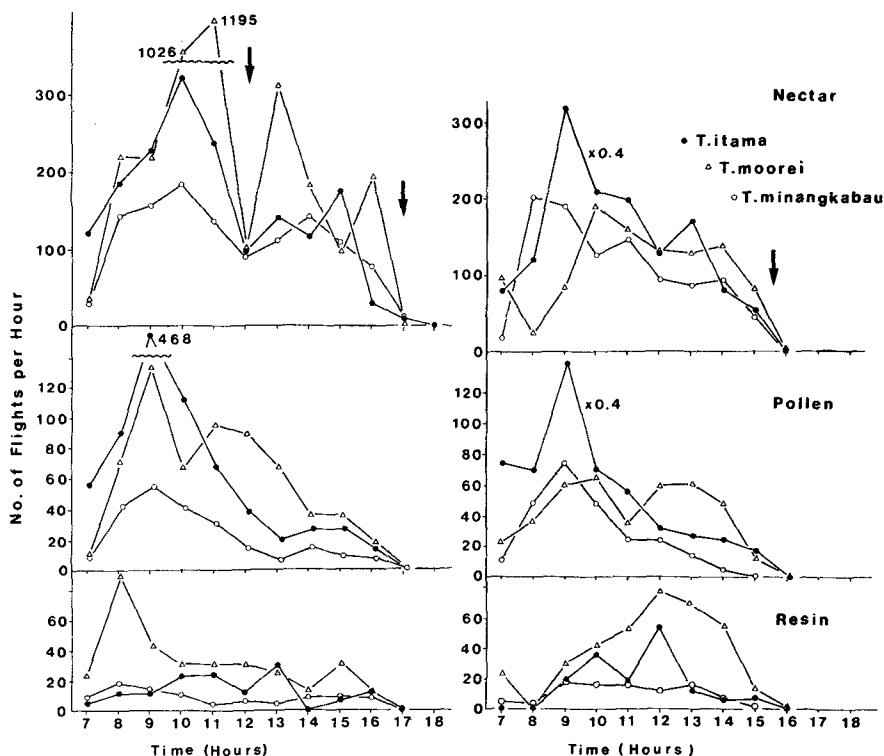


Fig. 1. Diurnal changes in foraging activities of colonies *Trigona itama*, *T. moorei* and pooled data of *Tm*₁, *Tm*₃ and *Tm*₄ (*T. minangkabau*) under adverse weather (indicated by arrows) on January 18 (left) and 19 (right). (Top) nectar, (middle) pollen and (bottom) resin.

nectar loads once decreased greatly around 1200 due to strong wind, and ceased at 1700 due to squall. On January 19 foraging ceased before 1530 also due to squalls. On January 22 and 23 foraging continued all day under fine weather conditions (Fig. 2). Below we use only data on January 22 and 23. *T. minangkabau* and *T. moorei* continuously collected nectar all day at similar intensity. *T. moorei* stopped foraging before 1800 although *T. minangkabau* and *T. itama* continued until 1830. This is due to the closure of the nest entrance at night which was characteristic of *T. moorei* alone. During 0900–1400 *T. itama* collected nectar more actively than at other times. Among the three species there was no statistical difference (*t*-test, $p > 0.05$) in the number of nectar loads in the morning and that in the afternoon. *T. minangkabau* and *T. moorei* collected pollen more actively in the morning than in the afternoon ($p < 0.01$). In *T. itama* this tendency was weak but was still significant ($p < 0.01$). *T. minangkabau* and *T. itama* collected resin all day; No significant difference was seen between the morning and the afternoon ($p > 0.05$). In *T. moorei*, we do not have sufficient data for a statistical test. In the three species, foragers stopped collecting resin earlier than nectar or pollen. As shown below, this is likely due to the longer time necessary to collect resin.

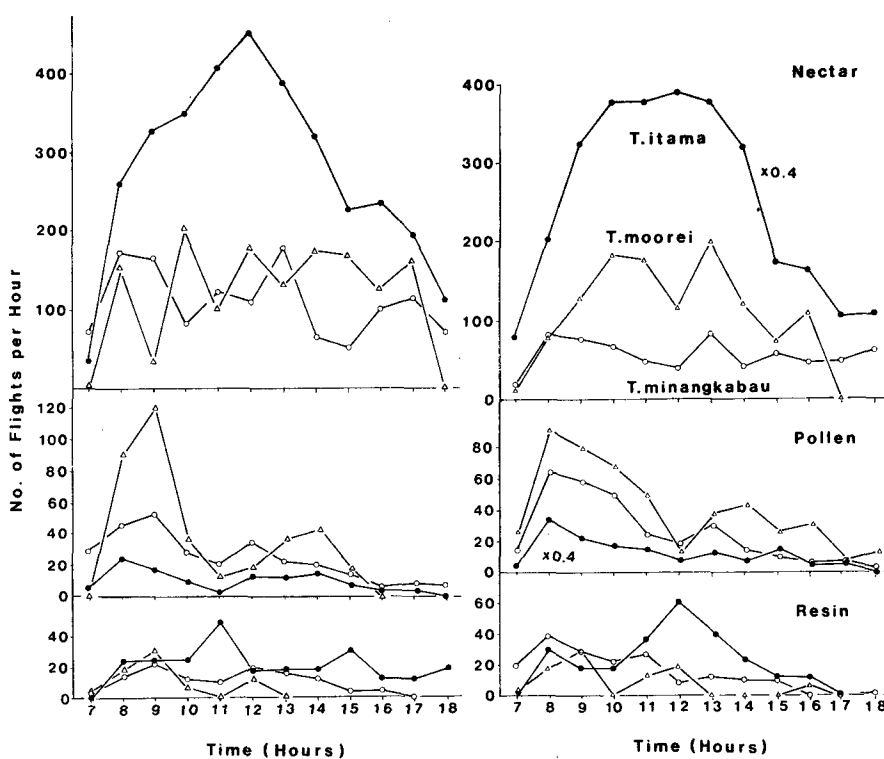


Fig. 2. Diurnal changes in foraging activities under favorable weather on January 22 (left) and 23 (right).

Amounts of Nectar and Pollen Loads

At departure workers of *T. minangkabau* carried, in the crop, 0.066 mg of sugar (concentration as sucrose % = 38, mean volume = $0.15 \mu\text{l}$, $s = 0.15$; $n = 24$). This amount of sugar was only 7% of sugar brought back by successful foragers.

In *T. minangkabau*, the mean volume of full nectar loads was $2.2 \mu\text{l}$. On January 11 and 14, the mean volume of nectar increased from about $0.7 \mu\text{l}$ during 0700–1000 to $1.5 \mu\text{l}$ during 1400–1600 and then decreased slightly (Fig. 3, upper). The maximum sugar concentration in nectar increased from about 30% in the morning to 60% in the afternoon. As a result the mean sugar weight brought back per flight increased in the afternoon. On February 18 and 19 (Fig. 3, lower), the mean volume of nectar was about $1.5 \mu\text{l}$ in the morning and dropped slightly after 1600. This drop is probably due to a bias from small sample size. The mean sugar concentration greatly increased after 1400, and variation of the sugar concentration was great also in the morning. The sugar weight increased until 1600 and then decreased slightly.

The mean volume of full nectar loads of *T. itama* was about $8.2 \mu\text{l}$. From early morning the mean volume of nectar was about $7 \mu\text{l}$ and decreased slightly after 1400 (Fig. 4, upper). In the morning the sugar concentration remained low and nearly constant at 27%. Although the minimum sugar concentration remained at the same

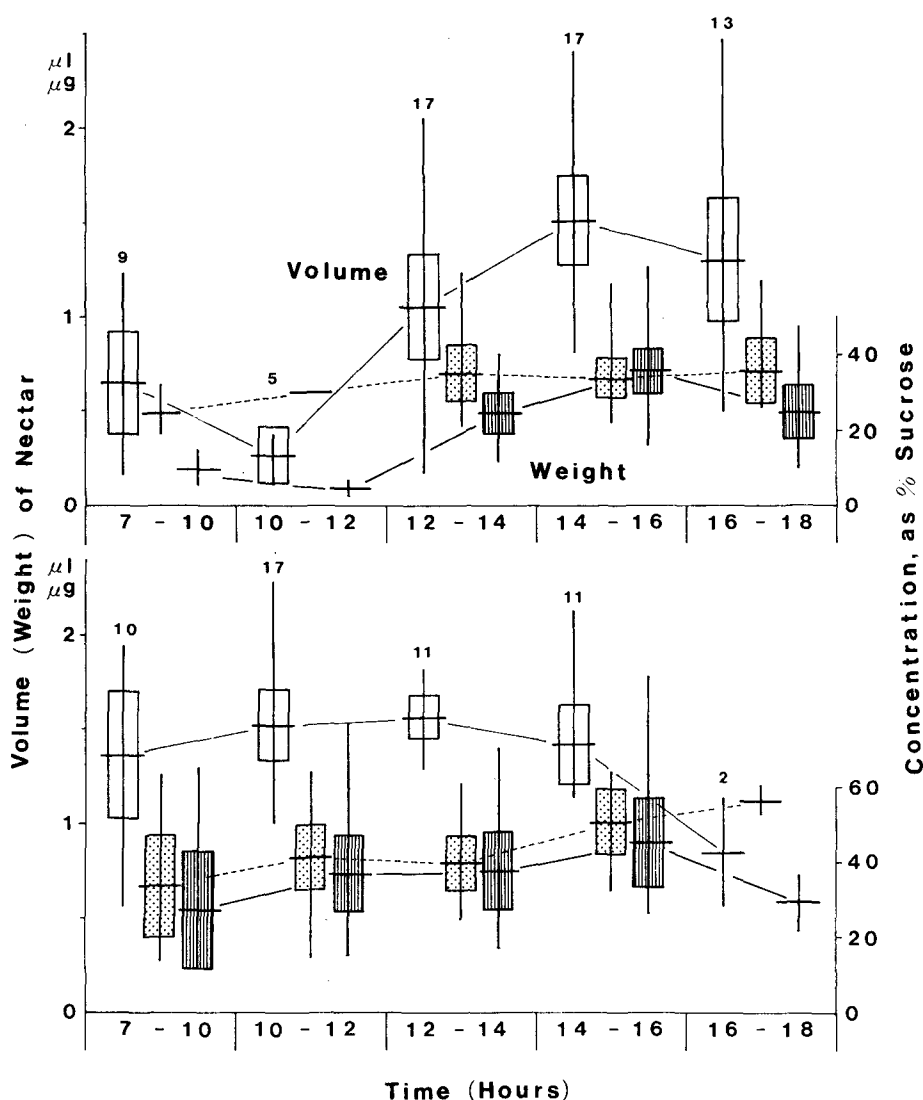


Fig. 3. Diurnal changes in volume of nectar (left in each period), concentration (middle) and weight (right) of sugar brought back by a foraging flight of *T. minangkabau*, in the Guest House (upper), in the SNS Laboratory (lower). Numerals indicate sample size. Boxes enclose 95% C.L. on each side of the mean. Vertical lines indicate range.

low level, the maximum exceeded 60% in the afternoon. The mean sugar concentration also increased over 40%. As a result the mean sugar weight increased gradually as time elapsed. The sugar concentration (c) slightly decreased proportionally to the volume (v); $c = -3.8v + 59$, $r = -0.43$.

In *T. moorei*, the mean volume of a full nectar load was $3.3 \mu\text{l}$. The volume of nectar, sugar concentration and sugar weight did not decrease throughout the day (Fig. 4, lower). Only *T. moorei* collected water (judged by the total dissolved solids $\leq 1.6\%$) at a rather high frequency (43% of total returns examined).

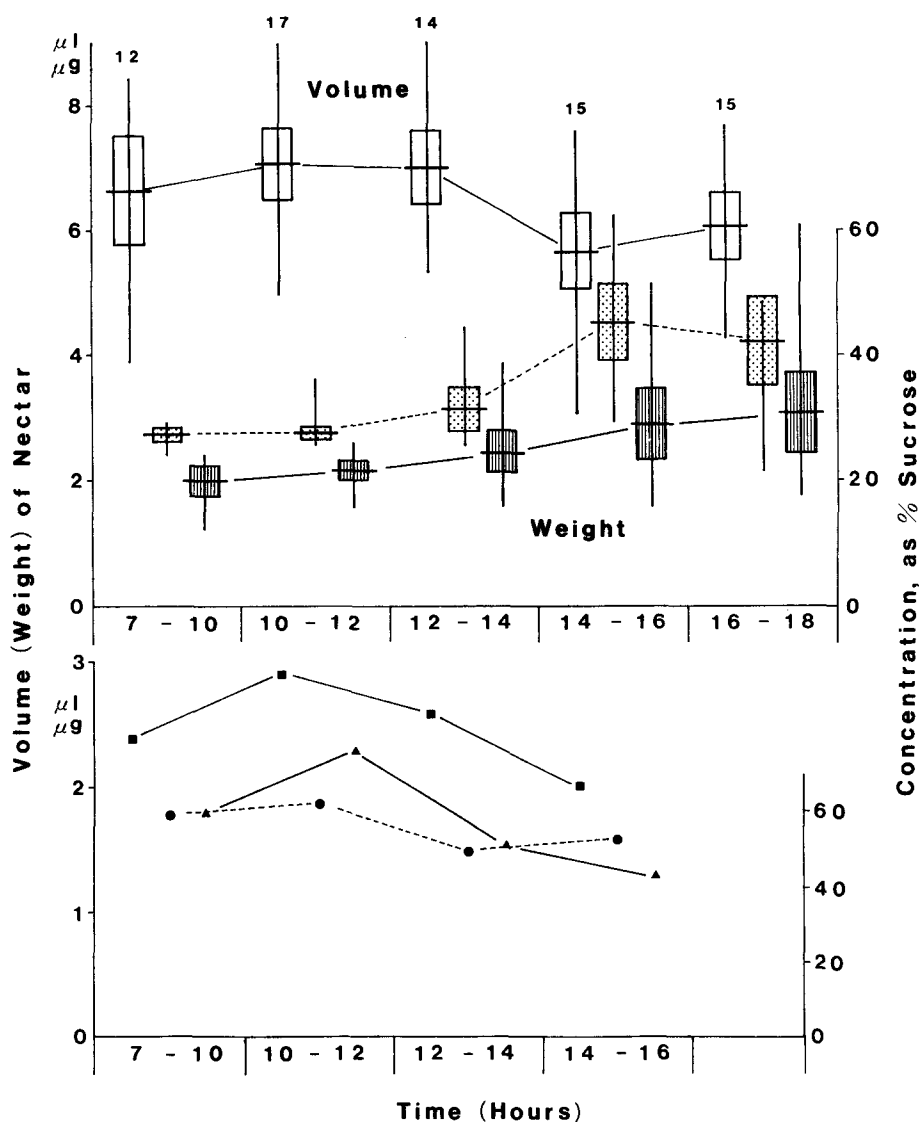


Fig. 4. Diurnal changes in volume of nectar, concentration and weight of sugar brought back by *T. itama* (upper) and *T. moorei* (lower). See Fig. 3 for more detail.

In Fig. 5 the volume (v_1) of two pollen loads on both sides of corbiculae brought back by a forager of *T. minangkabau* is plotted against the estimated volume of the pollen loads, v_2 (no. of grains \times volume of a grain), distinguishing grades of pollen load size (*L*, *M* and *S*). There was little overlap among grades of pollen load size on the v_1 - v_2 plane. The mean v_2 was 1.75 mm³ in *L*, 0.46 in *M* and 0.14 in *S*. Using these values of v_2 , we examined diurnal changes in amount of pollen per load. The mean v_2 increased from 0.70 in the morning to 0.84 in the afternoon, showing that the amounts of pollen per load also did not decrease in the afternoon.

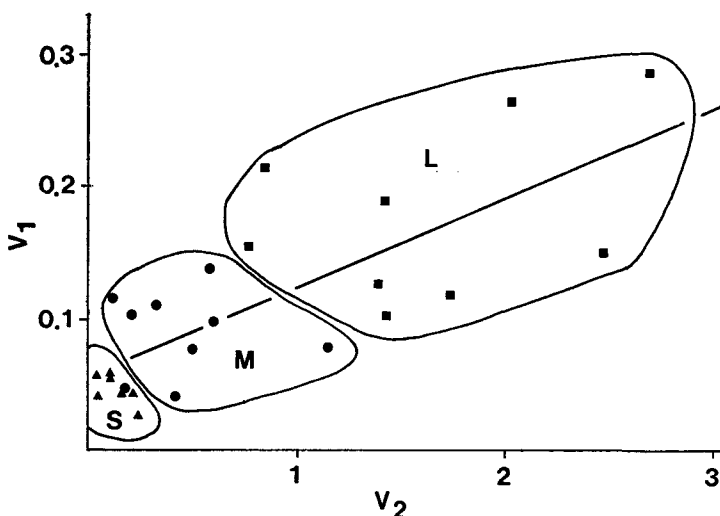


Fig. 5. Total volume of two pollen loads on corbiculae (v_1 mm³) plotted against the estimated volume of the pollen loads (v_2 mm³, no. of pollen grains \times volume of a grain), distinguishing grades of pollen load size. $v_1 = 0.26v_2 + 0.056$ ($r = 0.77$).

Flight Sequences of Individual Foragers

Figure 6 shows the flight sequence of an individual forager of *T. minangkabau*. On February 13 (upper) she started her first foraging flight at 1015 and came back at 1019 with no resource (N^-). It took 240 s for this flight (see right side of the figure). She stayed in the nest for 206 s until 1022 (see left side of the figure). On the second flight (104 s) she brought back fully laden nectar (N^{++}). The flight duration increased in the following flights. She stopped foraging after return with N^+ at 1211. On February 14 (Fig. 6, lower), she went out at 0914 firstly but came back with N^- . She brought back fully laden nectar (N^{++}) after a rather long flight (about 20 min) that started at 1122. The next flight was also long but, later, her flight duration became short and rather constant (about 10 min) until 1644. Furthermore the flight duration decreased gradually to about 2 min towards the dusk. She came back from the last foraging flight just before the sunset with N^+ . The total number of foraging flights in this day was 42 (maximum observed = 49 by a forager "W-P" on February 14). In contrast to February 13, she stayed in the nest for only about 2 min between two consecutive flights without any resting, from 1122 to 1813.

Another forager "TSCH" continued foraging pollen during whole periods available for foraging on February 11 and 13, without resting. Except for one or two rather long flights at the beginning and at the end of each day, flight duration was constant (12 min). On February 14 she came back from the first flight with P^+ . In the following 4 flights, the flight duration decreased. But then the flight duration increased with an increasing variation until 1415. After cessation of observation during 1420–1501, we found her homing with N^{++} after rather short flight duration. She sometimes brought back much nectar in crop with a little pollen on the corbiculae.

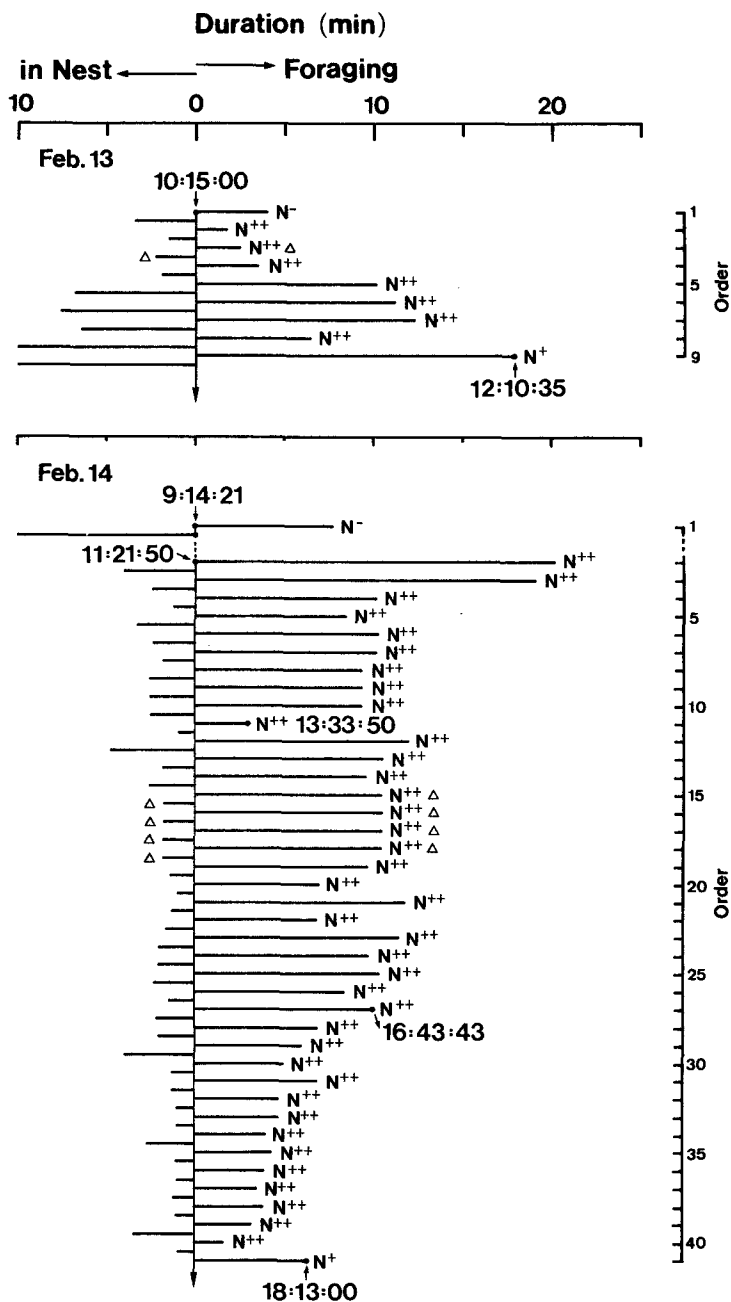


Fig. 6. Flight sequences of a forager "GOLD" on February 13 (upper) and on 14 (lower). Flight duration is shown on the right side of the figure, showing the kind of resources on the right end. Duration of stay in the nest is shown on the left side, truncated at 10 min. Time of some departures and returns, mainly the first departure and the last return, are shown in the figure in the form, hour:min:sec. Estimated values are shown by Δ . See text for more detail.

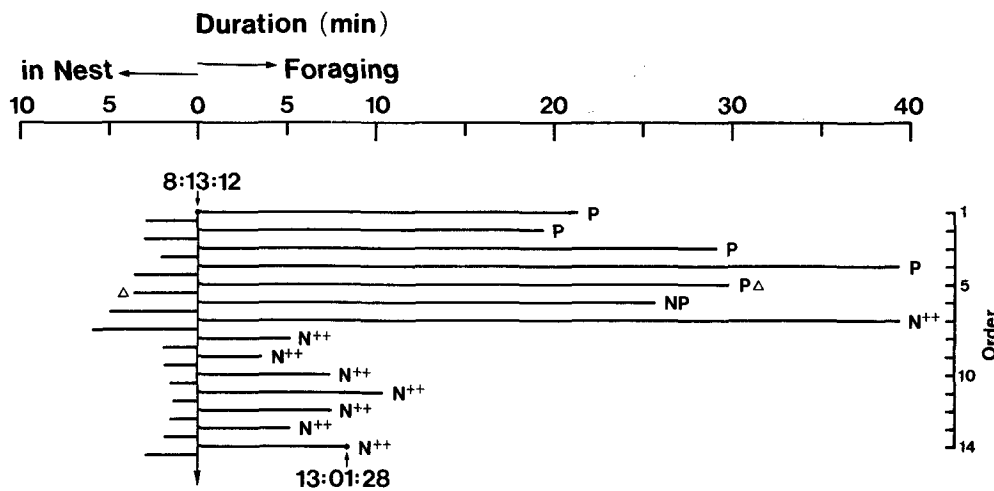


Fig. 7. Flight sequences of a nectar-pollen forager “B-P” on February 13. See Fig. 6 for details.

The clearest example of switching foraging from pollen to nectar was seen in a bee “B-P” (Fig. 7). After the start of foraging at 0813, she made 5 foraging flights for pollen. On the 6th flight she brought back both pollen and nectar. At 1158 she came back with fully laden nectar after the 7th, very long flight (40 min). After switching from pollen to nectar, her flight duration was shorten and more constant (7 min). We call the 6th and 7th flights “exploratory” flights and the 8th and later flights “exploitatory” flights (see Discussion).

In foraging resin, not only flight duration but also duration of staying in the nest were longer than those of pollen and nectar foragers. As a result, the number of daily flights was small. No foragers switched from resin to nectar and pollen or vice versa. On February 14 a worker, which made 5 foraging flights in the morning, came out from the nest and performed an exercise flight (*E*) at dusk. This means that *E* sometimes includes flights by experienced foragers.

All foragers did not make several successful daily foraging flights. For example, a worker made 4 foraging flights but collected *N*⁺ only once. Foragers which could not

Table 3. Combination of resources collected by 27 marked foragers of *T. minangkabau* during February 11–14. Active foragers are here defined as ones that performed at least one exploitatory flight.

Kind of resource	No. of foragers	No. of active foragers
Nectar	9	6
Nectar + Pollen	4	2
Pollen	1	0
Resin	5	3
Exercise	8	0
Total	27	11

Table 4. Statistics of duration (sec) for each foraging flight and other tasks: *S*=staying in nest (truncated at 1200 sec), *N*=return without any resources.

Tasks	Sample size	Mean	Standard deviation	Minimum value	5% point	95% point	Maximum value
<i>S</i>	213	202	164	52	61	524	1104
Exercise	8	95	75	7	15	206	232
<i>N</i> -	19	392	412	26	31	810	1849
Nectar	134	488	297	102	190	788	2363
Pollen	65	804	335	393	484	1283	2364
Resin	28	1352	671	570	603	2907	3756

collect resources after a few foraging flights in the morning tended to cease foraging in the afternoon.

Table 3 summarizes the combination of resources collected by individual foragers. As mentioned above some foragers collected both nectar and pollen, but resin foragers did not collect nectar and pollen. The percentage of active foragers that performed at least one exploitative flight was 40%.

Distance (d) from the nest to sites of exploited flowers can be estimated as follows. In the exploitative flights foragers constantly shuttle between the nest and the flower without resting. We observed the exploitative flights using feeders with ample nectar and obtained the following data (INOUE et al., unpub.): Mean speed (v) of flight = 1.17 m/s and mean duration (h) from arrival on feeder to departure = 46 s. Then the distance is estimated by $d = v(t - h)/2$ where t is the total flight duration shown in Table 4.

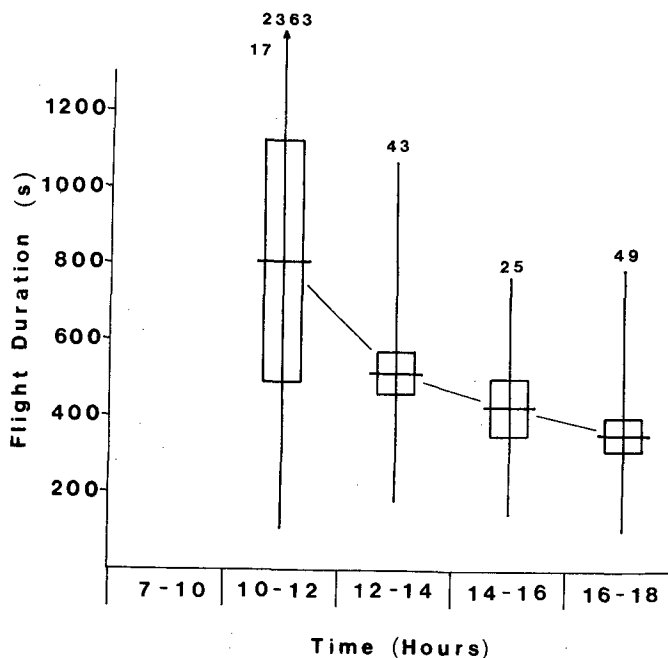


Fig. 8. Diurnal changes in flight duration for collecting nectar.

As 5% and 95% points of t was 190 and 788 respectively and flights in this range almost belonged to exploitative flights, 90% of the distances from the nest to exploited flowers distributed in the range from 84 to 434 m, with the mean = 258 m. This estimated range is much smaller than 8–10 km of honeybees (VISSCHER and SEELEY, 1982), 1.7 km of *Trigona capitata* and 2.6 km of *Melipona fasciata* (ROUBIK and ALUJA, 1983).

It took 1.7 times longer for pollen collecting than nectar (Table 4). Resin was the most time-consuming resource to collect (about 3x the time required for nectar). Prolonged foraging time for pollen and resin is not due to time travelling between the nest site and the site of resources but due to time for handling resources (INOUE et al., unpub.).

Mean flight duration for nectar collection (N^+) decreased from about 800 s in the morning to about 350 s during 1600–1800 (Fig. 8). There was no prolongation of flight duration in the afternoon.

DISCUSSION

Foraging Strategy

There were two foraging tactics of individual foragers of *T. minangkabau*: exploration and exploitation. In other studies with honey solution feeders we have observed the behavior of marked foragers at both nest and feeder (INOUE et al., unpub.). The foragers constantly shuttled between the nest and the feeder without resting. Such exploitative flights were also observed in this study; at the end of exploitative flights in the present study, the flight duration was prolonged and/or the amounts of resources brought back decreased. In these flights foragers were thought to try to find new resources. This quick switch to exploratory flights contrasts with honeybees. Honeybee workers which are trained to visit a feeder with ample honey solution continue visitation to the feeder for several days even after removal of honey solution (FRISCH, 1967). These exploratory flights again switched to exploitative flights after a return with fully laden resources. But some foragers which could not find rich resources by some exploratory flights in the morning stopped foraging in the afternoon.

All three stingless bee species studied here are small (*T. minangkabau*) or medium (*T. moorei* and *T. itama*), nonaggressive on natural flowers and unable to recruit members to rich feeders (confirmed in *T. minangkabau* and *T. moorei*). For such stingless bees, the individual quick switching of tactics between exploration and exploitation is important to increase foraging efficiency, although its efficiency in utilizing rich resources may be lower than bees which are able to recruit other members (ROUBIK, 1980; VISSCHER and SEELEY, 1982).

Diurnal Changes in Foraging Activity

Basic properties of floral nectar in temperate regions were clarified by CORBET (1978) and CORBET et al. (1979a, 1979b). Different groups of pollinators differ in their preferred concentration ranges of nectar. Eusocial bees such as honeybees and bumblebees utilize

nectar of 10–74%. Higher concentration is profitable for carrying to the nest but increases difficulty of imbibing due to high viscosity of nectar. On the other hand, flowers cannot secrete such highly concentrated nectar; the range of concentration of nectar soon after secretion is 12–34%. To increase the likelihood that the nectar will be at an appropriate concentration at a time of day when a suitable pollinator is active, flowers generally secrete nectar in the early morning and/or evening before commencement of pollinators' foraging. The nectar is concentrated by water evaporation in daytime.

If exploitative competition occurs for nectar secreted in a daily periodic manner as reviewed by CORBET (1978), the following phenomena must be observed. (1) Reduction of standing crop of floral nectar during the day. (2) Either prolongation of foraging duration of foragers which aim to fill their crops, or reduction of amount of nectar collected by foragers which fix foraging duration. (3) Peak foraging for time of day when resources are most abundant.

These three points were observed in bumblebees in temperate regions (HEINRICH, 1976). Bumblebees utilized >90% of nectar available per day in summer. Foraging durations of individual foragers were much prolonged in the afternoon (2 h). Even by this prolongation of foraging duration foragers could not fill their crops. The numbers of visits to flowers peaked in early morning and declined in midday, and again increased in the evening, as in the summer of temperate regions daytime became long enough for pollinators to utilize nectar just secreted in the evening.

In this study of three Sumatran stingless bees, sugar concentration of nectar carried to the nest was all about 30% in the morning, and its maximum value reached 60% in late afternoon. Nectar was condensed probably by water evaporation in daytime as reviewed by CORBET (1978). Volume of nectar carried per foraging flight was almost constant until 1600, and then slightly declined. As a result, the gain (weight of sugar) per flight increased as time elapsed in day. Flight duration for nectar collection in the afternoon decreased to less than half of that in the morning. Thus, the prolongation of foraging duration due to decrease of standing nectar did not occur in this study. This may reflect that only foragers which found rich resources continued exploitative flights in late afternoon. ROUBIK and BUCHMANN (1984) observed that the nectar of a shrub pollinated exclusively by stingless bees (*Melipona*) progressed from 35 to 60% sugar during the day, as did the nectar gathered by *Melipona* colonies, and suggested this has adaptive significance in increasing out-crossing at time of lower quantity nectar.

Nectar collection of the three Sumatran stingless bees did not peak in early morning as seen in bumblebees (HEINRICH, 1976); *T. itama* collected most actively in midday and *T. minangkabau* and *T. moorei* almost evenly over daytime. Resin was collected almost evenly over daytime by the three species. Pollen was actually collected more actively in early morning by the three species. But active pollen collection in the afternoon was observed in another study period (INOUE et al., unpub). Thus, the diurnal patterns of foraging activities change greatly, depending on kinds of resources and season differences,

and the peak foraging in early morning was not the case in this study. For *Melipona*, ROUBIK and BUCHMANN (1984) also observed peak nectar harvest in late morning or early afternoon similar to *T. ilama* and peak pollen harvest in early morning. Thus typical exploitative competition observed in bumblebees for flowers containing maximum nectar reward at early morning (HEINRICH, 1976) did not occur in either *Trigona* or *Melipona*.

The above discrepancies between the expectation by CORBET (1978) and the observations in the present study may lie in that some tropical plants secrete nectar after commencement of pollinator foraging. Actually CORBET and WILLMER (1981) showed that ornithophilous flowers in Costa Rica secreted nectar actively before and during peak visitation of pollinators (late morning). ROUBIK and BUCHMANN (1984) showed that the shrub pollinated by *Melipona* secreted more than 30% of total daily nectar production after commencement of foraging. We need further studies of nectar secretion patterns of tropical plants, to understand diurnal foraging patterns of stingless bees.

Net Energy Gain of Exploitative Flight

In *T. minangkabau* the range of exploitative flights for nectar was estimated to be about 0.5 km from nest. This value was much smaller than honeybees and some other stingless bees. To clarify factors determining this foraging range, we calculate the caloric gain of a nectar load and the caloric cost for the flight, using methods similar to HEINRICH (1979).

The average body weight of a worker of *T. minangkabau* with empty crop (W_b) was 4.2 mg (SAKAGAMI et al., 1983). The average volume (V_n) of a nectar load of exploitative flight was 1.5 μ l (this study). The weight (W_n) of a nectar load with sugar concentration s is given by $gV_n/(s+g-sg)$ and the sugar weight (W_s) in a nectar load by sW_n , where g is the specific gravity of sucrose (=1.552). Then caloric gain of a nectar load (G) becomes $3.9 W_s$ cal.

TUCKER (1970) showed that the unit cost (C_f) for an insect with body weight W mg to move 1 m by flight was well expressed by $C_f=28.8W-0.227$. We use his estimation equation for calculation of flight cost. As the body weight is W_b at going flight and W_b+W_n at return flight, total cost (C) of a flight trip to the flower d m distant from the nest is given by,

$$\begin{aligned} C &= \{C_f W_b + C_f (W_b + W_n)\}d \\ &= 28.8\{W_b^{0.773} + (W_b + W_n)^{0.773}\}d \end{aligned}$$

C is a linear function of d and we call its coefficient C_u . As already shown in Results, the duration (t) of exploitative flights is given by $t=2d/v+h$, where v is the flight speed (=1.17 m/s) and h is time imbibing nectar (=46 s). Then, ignoring the cost for imbibing, the net gain (G_n) per unit time is given by,

$$G_n = (G - Cd)/(2d/v + h)$$

Figure 9 shows the net gain of an exploitative flight of *T. minangkabau*. G_n decreases in a hyperbolic manner with increase of d . When the sugar concentration equals the

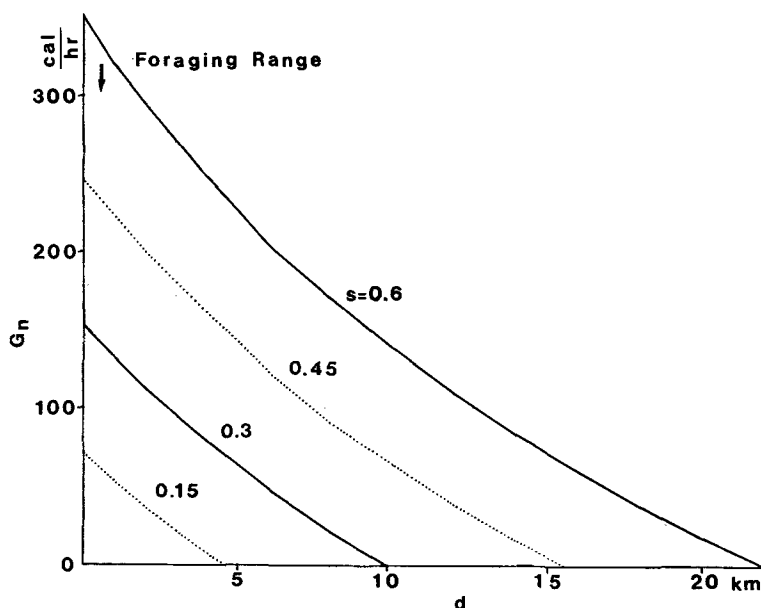


Fig. 9. Net gain (G_n) per unit time of exploitative flights for nectar, of which sugar concentrations (s) are 0.6 (observed maximum), 0.45, 0.3 (observed minimum) and 0.15, in *T. minangkabau* plotted against distance (d) between flower and nest. See text for details.

maximum observed value (0.6), the critical distance over which G_n becomes negative is 22 km. But even the sugar concentration decreases to the observed minimum (0.3), the critical distance is 10 km. The observed foraging range (0.5 km) is far smaller than these values and the flight cost in this range is $<5\%$ of the caloric gain. Generally, under the strong consumption of floral resources foragers must expand their foraging range until the critical distance within which foraging flights give the positive net gain, because the consumption usually occurs from area near to the nest. But this stingless bee confined the foraging range into a rather small area around the nest. This means that the exploitative competition against floral resources is not keen in this species in this habitat condition.

The amount of sugar carried out at commencement of foraging flight (0.066 mg) provides with energy for flight for about 3 km. Therefore this amount may be enough to support not only exploitative flights but also exploratory flights. This supports HEINRICH (1979)'s idea that bees should leave the hive nearly empty, with just enough fuel to get where they want to go, plus a little resource for emergencies.

SUMMARY

The foraging behavior of three stingless bees, *Trigona* (*Tetragonula*) *minangkabau*, *T. (Trigonella)* *moorei* and *T. (Heterotrigona)* *itama*, was studied to describe patterns of resource harvest in disturbed forest areas in Sumatra, Indonesia.

1. Average daily total number of foraging flights per colony was 1200 in *T.*

minangkabau, 2400 in *T. moorei* and 7000 in *T. itama* and it was proportional to colony population size. Foragers collecting nectar, pollen or plant resin were respectively 70–80%, 10–20% and <10% in the three species. Pollen was collected most in the morning. Nectar collection peaked in midday in *T. itama* but continued almost evenly until dusk in *T. minangkabau* and *T. moorei*. Resin was collected evenly throughout day.

2. In all the three species the volume of a nectar load carried by a returning forager did not decrease until 1600, followed by slight decline. In the morning the sugar concentration of nectar was almost constantly 30%, and in the afternoon its maximum value reached 60% although some remained 30%. As a result, the mean sugar weight in a nectar load gradually increased until dusk.

3. In *T. minangkabau*, resin was collected by specialized foragers. Nectar foragers switched to collect pollen and vice versa. There were two types of foraging: “*exploitatory*” flights, the repetition of short, rather constant flights bringing back full resource loads, and “*exploratory*” flights, prolonged flight and/or reduction in amount of resources carried. Exploitative flights followed the exploratory flights which led to discovery of rich sources. Mean duration of exploitative flights was 7 min during nectar collection, 12 min for pollen and 23 min for resin. Sites of exploited flowers were estimated to be 84–434 m distant from the nest site. Mean duration of flights for nectar collection was 13 min in the morning and 6 min in the late afternoon.

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⁽¹⁾ This species was newly described as *Trigona (Tetragonula) minangkabau* by SAKAGAMI and INOUE (1985).

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スマトラのハリナシバチ 3 種の採餌行動

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ハリナシバチの採餌行動は、主にコミュニケーションシステムおよび餌（蜜、花粉）、巣材料（樹脂）をめぐる競争という観点から中南米で研究されてきた。本研究はこれまでまったく研究されていない東南アジアのハリナシバチの採餌行動の基本的特徴について報告する。調査はスマトラの二次林に分布する 3 種のハリナシバチ、*Trigona* (*Tetragonula*) *minangkabau*, *T.* (*Trigonella*) *moorei*, *T.* (*Heterotrigona*) *itama* についておこなった。

コロニーごとの日当たり平均採餌飛行回数は、*T. minangkabau* で1200回、*T. moorei* で2400回、*T. itama* で7000回であり、これはワーカー数にほぼ比例していた。3 種とも採餌飛行の70-80%は蜜採集のためであり、10-20%が花粉採集、樹脂採集は10%以下だった。花粉は3 種とも主に午前中に採集した。蜜採集は *T. itama* では正午頃に最も活発だったが、他の 2 種では日中ずっと続いた。樹脂は3 種とも1 日中採集した。

1 回の飛行で採集される蜜量は夕方まで少しずつ増加し続けた。糖度は午前中30%と一定していたが午後には最高60%と濃くなった。その結果、1 回当たり採集される糖量は夕方になるほど増加した。

採餌飛行には2つのタイプがみられた。「開発」飛行 (exploitatory flight) では、比較的短くかつ一定した飛行のあと、運ぶうる最大限に近い量を持ち帰った。「探検」飛行 (exploratory flight) では飛行時間が長くなったり、持ち帰る量が少なかったりしたが、豊富な資源をみつけると開発飛行に切り換わった。この切り換えは個体ごとに行われ、ミツバチにみられるようなコミュニケーションシステムは存在しなかった。採餌に利用される範囲は巣から約 0.5 km とミツバチの 5-10 km などにくらべ、非常に狭かった。

HEINRICH (1976) の観察によると、マルハナバチでは消費による競争がおこるため、早朝に採餌のピークがあり、午後には飛行時間も延び、採集量も減少するとのことであるが、本研究ではこうした消費を通じての資源をめぐる競争は観察されなかった。