Apidologie 33 (2002) 303–314

DOI: 10.1051/apido:2002016

Original article

Foraging activity and pollen diets of subterranean stingless bee colonies in response to general flowering in Sarawak, Malaysia

Teruyoshi NAGAMITSU[a]*, Tamiji INOUE[b]

[a] Hokkaido Research Center, Forestry and Forest Products Research Institute, Hitsujigaoka 7, Toyohira, Sapporo 062-8516, Japan
[b] Center for Ecological Research, Kyoto University, Kamitanakami Hiranocho, Otsu 520-2113, Japan

(Received 17 July 2001; revised 13 November 2001; accepted 28 January 2002)

Abstract – General flowering is a type of supra-annual mast flowering at community level in Southeast Asia, which occurred in 1996 after a four-year interval in northern Sarawak, Malaysia. To examine foraging responses to general flowering, foraging activity and pollen diets of subterranean stingless bee (*Trigona* spp.) colonies were compared over 3 periods in 1994 and 1996. Among variables of foraging activity (frequency of forager returns, proportions of nectar and pollen foragers), only the frequency of forager returns was significantly higher in 1996 than in 1994. The proportion of nectar foragers differed significantly among periods within a year. Among variables of pollen diet breadth (pollen type richness, diversity and evenness indices), none differed significantly between years or among periods. Pollen diet similarity between colonies did not differ significantly between years, although it differed among periods.

lowland mixed dipterocarp forests / foraging / general flowering / nectar / pollen diet / Sarawak / *Trigona*

1. INTRODUCTION

General flowering is a type of community-scale mast flowering that is unique to Southeast Asia and is synchronized at irregular intervals of 2–10 years among most plant species of lowland mixed dipterocarp forests (Appanah, 1985; Ashton et al., 1988; Yasuda et al., 1999). Nearly all plant species in the lowland mixed dipterocarp forests are pollinated by animals (Momose et al., 1998). General flowering may have

* Correspondence and reprints
E-mail: nagamit@ffpri.affrc.go.jp

great impact on population and behavior of pollinators due to changing availability of their resources (Sakai, 2001).

Among animal pollinators, social bees (Apidae, Hymenoptera) are the most common (Momose et al., 1998). Stingless bees (*Trigona*, *Lisotrigona* and *Pariotrigona* spp.) are most abundant among social bees in Southeast Asia (Inoue et al., 1990; Michener, 2000). Their resident colonies depend on flowers for all their food and forage throughout the year. Thus, stingless bees in lowland mixed dipterocarp forests are suitable subjects with which to evaluate pollinator responses to the changing availability of floral resources.

Although little is known about how stingless bees respond to general flowering, specific response mechanisms of other pollinators, such as thrips (Thysanoptera), chrysomelid beetles (*Monolepta* spp., Chrysomelidae) and giant honeybees (*Apis dorsata*, Apidae), have been proposed (Appanah, 1993; Momose et al., 1998). Thrip populations rapidly increase, due to their short generation time and high fecundity (Appanah and Chan, 1981). Chrysomelid beetles seem to change their food types from leaves to flowers in response to general flowering (Sakai et al., 1999a). Giant honeybees immigrate to lowland mixed dipterocarp forests as soon as general flowering starts, and when it finishes they leave (Itioka et al., 2001). However, stingless bees show none of these responses, i.e., they do not show rapid population growth (Inoue et al., 1993), change food types from nectar and pollen to others, or migrate over a long distance (Inoue et al., 1984).

Previous studies of flowering plants (Sakai et al., 1999b) and stingless bees (Nagamitsu et al., 1999) in a lowland rain forest in northern Sarawak were conducted during 1992 and 1996. Extremes in the proportion of flowering plants were observed in 1994 and 1996. In 1994, less than 5% of plant species and individuals flowered, while in 1996 there was a general flowering event in which more than 17% of plant species and individuals flowered. This difference provided an opportunity to investigate the foraging response of stingless bee colonies to general flowering. Data obtained on the foraging activity and pollen diets in 1994 and 1996 were used to address two questions: (1) As the density of flowering plants increases, do stingless bee colonies increase the frequency of forager returns and the proportion of nectar and pollen foragers? (2) As the species diversity of flowering plants increases, are there corresponding increases in pollen diet breadth of colonies and decreases in pollen diet similarity between colonies?

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted in the Canopy Biology Plot (CBP, 8 ha: 200 × 400 m) established in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E; altitude 150–250 m; Inoue et al., 1995).

Flowering phenology of 576 individual plants representing 305 species in 56 families in the study site was monitored from 1992 to 1996 in a previous study (Sakai et al., 1999b). In 1992, general flowering occurred, and flowering of 12% of the species and 11% of individuals was observed in August 1992. From September 1992 to February 1996, the proportions of flowering species and individuals were less than 5% and 3%, respectively, except for minor peaks rising to 8% and 7%, respectively, in February 1993. After March 1996, the number of flowering plants rapidly increased, and the proportion of flowering species and individuals reached 21% and 17%, respectively, in May 1996. After a reduction of flowering in July 1996, 10% of the species and 8% of individuals were

observed to flower in October 1996 (Sakai et al., 1999b). Most of the emergent, canopy, and subcanopy trees flowered only in 1996, while lianas, epiphytes, and plants in the understory and canopy gaps tended to bloom more frequently (Sakai et al., 1999b). Furthermore, the magnitude of a reproductive event, measured by the relative number of flowers and fruits of each observed plant, was also larger in 1996 than in the years 1993–1995 (Sakai et al., 1999b). These facts indicate that the number of plant species in the forest, the number of flowering plants of each species, and the amount of floral resources of each plant increased in the general flowering episode.

Stingless bee colonies at underground nest sites were investigated, because foragers arriving at the nest entrances on the forest floor were easily observed. Subterranean colonies in CBP were surveyed in 1994, and 11 colonies of five *Trigona* species (one of *T. thoracica*, seven of *T. collina*, two of *T. rufibasalis*, one of *T. melanocephala*, and one of *T. melina*) were observed (Nagamitsu and Inoue, 1997). Among them, six colonies persisted throughout 1992 and 1996. These colonies designated as colonies A, B and C of *T. collina*, colony D of *T. rufibasalis*, colony E of *T. melanocephala* and colony F of *T. melina* were selected for measurement of foraging activity.

2.2. Foraging activity

Foraging activity of each selected colony was measured in three periods (22–23 June, 10–13 August and 17–19 September) in 1994, and in three periods (15–18 May, 4–8 August and 19–23 August) in 1996.

To determine the frequency of forager returns to a colony, the nest entrance of the colony was closed with cotton cloth for between 15 and 40 min three times (at approximately 07.30 h, 10.30 h, and 14.30 h local time) on a single day in each period. The closure times varied because three colonies were sampled at approximately the same time, and some colonies took longer to count than others. The bees arriving during the closure period were counted as follows. A nest was closed and the time of closure (T1) was recorded. Arriving bees would then hover or land near the nest entrance. Approximately 10–35 min after a nest was closed, the bees were gently collected with a hand net for about two minutes, and approximately two more minutes were used to count the bees in the net. To count the bees, the net was flattened, and the number of bees (N1) was counted with a hand counter. During the counting, a few bees would typically arrive at the nest. The number of these late-arriving bees (N2) was visually counted. The time at which this count ended (T2) was recorded, and the nest closure was removed. The frequency of forager returns was expressed as $(N1 + N2) / (T2 - T1)$.

Of the bees collected in the net, 20 were kept for determining the proportions carrying nectar and pollen loads, and the rest were released. The numbers carrying pollen (visible corbicular loads on the tibia of the hind leg) and nectar (visible as a drop of nectar at the mouth after pressing the abdomen) were recorded. Resin foragers were discriminated from the pollen or nectar foragers. Collection with the net was quite gentle, and did not appear to affect either the pollen or nectar loads. The pollen loads were collected for later analysis. Because the colonies usually have more than a thousand of workers (Sakagami et al., 1983), the sampling of a total 60 foragers from a colony was not thought to have any significant effect on the colony.

2.3. Pollen diets

Pollen loads were collected from the sampled foragers. Only colonies from which more than five pollen foragers were sampled in every period were examined.

Three colonies (colonies C, E, and F) met this criterion. After acetolysis (Erdtman, 1960), 200 pollen grains of the pollen load of each forager were observed with a light microscope, and classified by morphology into taxonomically distinct pollen types (Huang, 1972; Roubik and Moreno, 1991; Tissot et al., 1994). The most abundant pollen type in the pollen load of a forager was regarded as the main pollen source of this forager. These samples were parts of a data set that has been used in Nagamitsu et al. (1999). In the present study, the samples were examined in detail, and were analyzed with different methods.

Based on these observations, we obtained the number of foragers N_{ijky}, of colony i, with pollen type j, of each pollen source in collection period k, in year y. To measure the diversity and evenness of the pollen diets of the colonies, we calculated Shannon-Weaver's diversity H_{iky} and Pielou's evenness J_{iky} (Pielou, 1966), of colony i, in period k, in year y, as follows:

$$H_{iky} = -\Sigma_j[\{N_{ijky} / \Sigma_j(N_{ijky})\} \ln\{N_{ijky} / \Sigma_j(N_{ijky})\}] \quad (1)$$

$$J_{iky} = H_{iky} / \ln(L_{iky}) \quad (2)$$

where pollen type richness L_{iky} is the number of pollen types observed in colony i, in period k, in year y.

To measure the diet similarity between colonies, we calculated Morisita's similarity index $C_{ii'ky}$ which is not affected by sample size (Morisita, 1959), in period k, in year y, between colonies i and i', as follows:

$$C_{ii'ky} = 2\,\Sigma_j(N_{ijky}\,N_{i'jky}) / (\lambda_i + \lambda_{i'})\,\Sigma_j(N_{ijky})\,\Sigma_j(N_{i'jky}) \quad (3)$$

$$\lambda_i = \Sigma_j\{N_{ijky}\,(N_{ijky} - 1)\} / \Sigma_j(N_{ijky})\,\{\Sigma_j(N_{ijky}) - 1\} \quad (4)$$

$$\lambda_{i'} = \Sigma_j\{N_{i'jky}\,(N_{i'jky} - 1)\} / \Sigma_j(N_{i'jky})\,\{\Sigma_j(N_{i'jky}) - 1\}. \quad (5)$$

2.4. Data analysis

Nested-ANOVA with period nested in year was performed to test differences in variables of foraging activity and pollen diets. Year and time were treated as fixed factors, and period, colony and colony pair as random factors. Three variables of foraging activity (frequency of forager returns and proportions of nectar and of pollen foragers) were analyzed using a model:

$$Y_{ykit} = \mu + year_y + period_{k(y)} + colony_i + year \times colony_{yi} + period \times colony_{ik(y)} + time_t + year \times time_{yt} + period \times time_{tk(y)} + colony \times time_{it} + year \times colony \times time_{yit} + \varepsilon_{ykit}. \quad (6)$$

To stabilize the variance, the frequency of forager returns was square-root transformed, and the proportions of nectar and pollen foragers were arcsine-square-root transformed. Three variables of pollen diet breadth (pollen type richness, diversity index and evenness index) were analyzed using a model:

$$Y_{yki} = \mu + year_y + period_{k(y)} + colony_i + year \times colony_{yi} + \varepsilon_{yki}. \quad (7)$$

Pollen diet similarity of two colony pairs (colony C-E and E-F) was analyzed using a model:

$$Y_{yki} = \mu + year_y + period_{k(y)} + colony\ pair_i + year \times colony\ pair_{yi} + \varepsilon_{yki}. \quad (8)$$

Similarity index was arcsine-square-root transformed, because its variance increases as its mean approaches 0.5 from 0 or 1 (Ricklefs and Lau 1980).

3. RESULTS

3.1. Foraging activity

The frequency of forager returns differed between 1994 and 1996 ($F_{1,4} = 23.8$, $P = 0.008$), although the proportions of nectar and pollen foragers did not ($F_{1,4} = 2.1$ and 0.9, $P = 0.218$ and 0.391, respectively). Forager returns were more frequent in 1996 than in 1994 (Fig. 1).

The proportion of nectar foragers differed among periods within a year ($F_{4,20} = 9.0$, $P < 0.001$). Differences in the frequency of forager returns and proportion of pollen foragers were not significant marginally ($F_{4,20} = 2.4$ and 2.7, $P = 0.088$ and 0.060, respectively). Among three periods in each year, the frequency of forager returns and the proportion of nectar foragers showed a consistent pattern. They were highest on 17–19 September in 1994 and on 19–23 August in 1996, and were lowest on 10–13 August in 1994 and on 4–8 August in 1996 (Figs. 1 and 2). The proportion of pollen foragers showed the same pattern in 1996 (Fig. 3). In 1994, however, it was highest on 22–23 June, and was lowest on 17–19 September.

All the variables of foraging activity were significantly different among times within a day ($F_{2,8} > 6.6$, $P < 0.020$) and among colonies ($F_{5,20} > 2.7$, $P < 0.050$). Among three times in a day, the frequency of forager returns was highest at 10.30 h, and was lowest at 14.30 h (Fig. 1). The

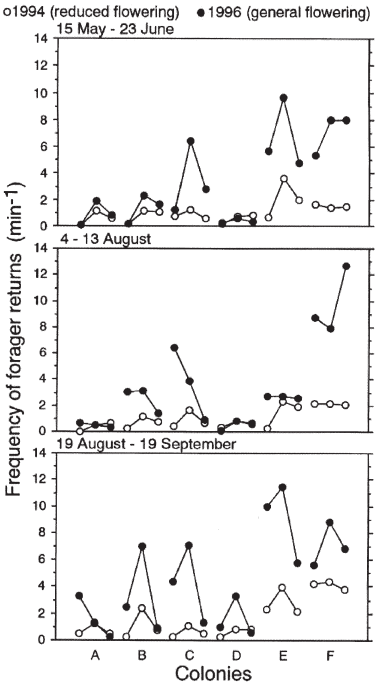

Figure 1. Foraging activity of *Trigona* colonies, A-C: *T. collina*, D: *T. rufibasalis*, E: *T. melanocephala* and F: *T. melina*. Lines connect observations at 07.30 h (left), 10.30 h (center) and 14.30 h (right).

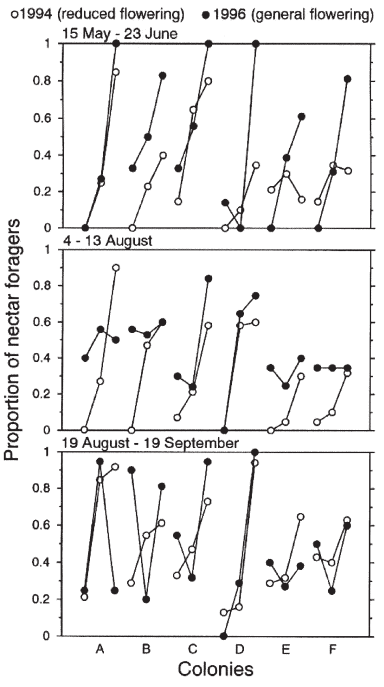

Figure 2. Nectar foraging of *Trigona* colonies, A-C: *T. collina*, D: *T. rufibasalis*, E: *T. melanocephala* and F: *T. melina*. Lines connect observations at 07.30 h (left), 10.30 h (center) and 14.30 h (right).

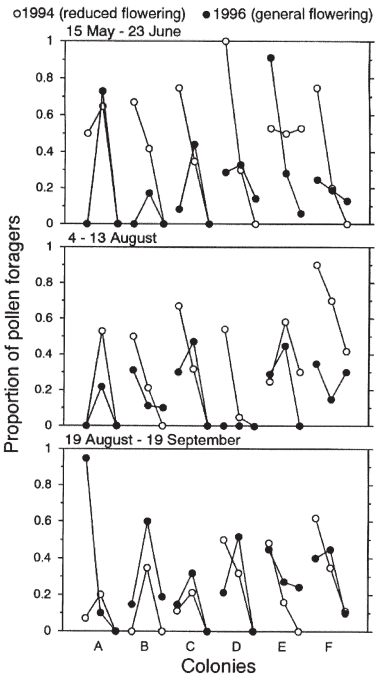

Figure 3. Pollen foraging of *Trigona* colonies, A-C: *T. collina*, D: *T. rufibasalis*, E: *T. melanocephala* and F: *T. melina*. Lines connect observations at 07.30 h (left), 10.30 h (center) and 14.30 h (right).

proportions of nectar and pollen foragers showed opposite diurnal patterns (Figs. 2 and 3). At 07.30 h, nectar foragers were fewest, and pollen foragers were most. At 14.30 h, nectar foragers were most, and pollen foragers were fewest.

Colonies E (*T. melanocephala*) and F (*T. melina*) were characterized by higher frequency of forager returns, lower proportion of nectar foragers and higher proportion of pollen foragers, compared with other colonies (Figs. 1, 2 and 3). Colonies A, B and C (*T. collina*) showed higher proportion of nectar foragers and lower proportion of pollen foragers (Figs. 2 and 3). Colony D (*T. rufibasalis*) was characterized by lower frequency of forager returns (Fig. 1).

3.2. Pollen diets

In a total of 307 pollen loads collected from colonies C, E and F, 74 pollen types were distinguished (Appendix). Of the 74 pollen types, 46 were identified as belonging to 18 plant families. The most abundant pollen types belong to Araceae, followed by Annonaceae and Euphorbiaceae. Pollen diets of colony C were characterized by utilization of Fabaceae (pollen type F1: *Mimosa* spp.) and Passifloraceae (pollen type G1: *Passiflora* spp., Appendix). Main pollen sources of colonies E and F were Annonaceae (pollen type B1: unknown genus) and Araceae (pollen type A1: unknown genus), respectively. Only pollen type C1 of Euphorbiaceae was shared among the three colonies.

Although pollen type richness did not differ significantly between years and among periods ($F_{1,4} = 0.2$, $P = 0.716$ and $F_{4,8} = 1.8$, $P = 0.230$, respectively), it differed among colonies ($F_{2,8} = 5.1$, $P = 0.037$).

Pollen type richness was highest in colony F (mean ± SD, 7.17 ± 1.47), followed by colony E (6.83 ± 1.17) and colony C (4.83 ± 1.72). Diversity and evenness indices of pollen diets did not differ

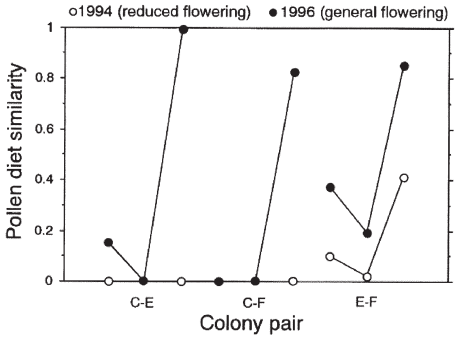

Figure 4. Morisita's similarity index of pollen diets between colonies C: *T. collina*, E: *T. melanocephala* and F: *T. melina*. Lines connect observations in three periods from 15 May to 23 June (left), from 4 to 13 August (center) and from 19 August to 19 September (right).

significantly between years, among periods and among colonies.

Pollen diet similarity of two colony pairs C-E and E-F was examined. Although similarity index did not differ significantly between years ($F_{1,4}$ = 2.8, P = 0.169), it differed among periods and between colony pairs ($F_{4,4}$ = 18.4, P = 0.008 and $F_{1,4}$ = 38.5, P = 0.003, respectively). Similarity index was extremely high on 19–23 August 1996 among six periods (Fig. 4). Similarity index between colonies E and F was higher than that between C and E as well as that between C and F.

4. DISCUSSION

This study demonstrates three main results. First, among variables of foraging activity and pollen diets, only the frequency of forager returns differed between the general flowering year and the other year. Second, the proportion of nectar foragers and pollen diet similarity changed among periods within a year. Third, pollen diet breadth was temporally stable.

4.1. Difference in frequency of forager returns between years

In addition to the first result, the frequency of forager returns changed in the different temporal scales: between years and among times within a day. The frequency of forager returns can be determined at least two factors: the number of foragers in individual colonies and the frequency of foraging trips by individual foragers. Although these factors can not be discriminated in this study, importance of the two factors for changes in the frequency of forager returns may differ between the two temporal scales.

Within a day, forager returns were frequent in the morning, which is consistent with diurnal patterns in foraging activity observed in other *Trigona* species (Inoue et al., 1985). Changes in foraging frequency of individual foragers are responsible for the diurnal changes, because forager population of individual colonies seems stable during a day.

In longer temporal scales than duration of worker development, forager population can change. Post-emergence development of workers has been known in *T. laeviceps* (Sakagami et al., 1983), and foraging begins a month after emergence in *T. minangkabau* workers (Inoue et al., 1996). Thus, growth of forager population may require duration of more than a month. It is known that breeding of new workers of *Melipona* species begins as pollen harvests increase (Roubik, 1982). Growth of forager population in 1996 is possible during the beginning of the general flowering in March and the observation period in June. Difference in forager returns between 1994 and 1996 is so large that the ranges of diurnal variation are often apart between the years. These facts suggest that growth of forager population is responsible for the increase in forager returns in a general flowering year.

4.2. Changes in proportions of nectar and pollen foragers and pollen diet similarity

The second result suggests that allocation of foragers to nectar and pollen collection and pollen diet similarity respond to resource fluctuation in temporal scales much shorter than general flowering cycles. Pollen collection peaks in the morning, and nectar collection follows later in the day, which agrees with observations on other *Trigona* species (Inoue et al., 1985; Roubik and Buchmann, 1984). This diurnal pattern is thought to reflect both a depletion of pollen quantity and an increase in nectar quality during the day, which is supported by the decreasing amounts of pollen and the increasing sugar concentration of nectar in

flowers during the daytime (Nagamitsu and Inoue, 1997).

In seasonal temporal scales, abrupt flowering events in local spatial scales may affect foraging activity and pollen diet similarity. On 19–23 August 1996, both nectar and pollen foragers were relatively abundant, and pollen diet similarity was extremely high. This high similarity is mainly due to common utilization of a single pollen type. These findings can be interpreted as foragers from different colonies aggregated to abundant flowers of a plant species blooming simultaneously within their foraging range. Although Eltz et al. (2001) examined pollen diets of the same *Trigona* species as we did in our study, such an extreme increase in diet similarity was not observed during the three months of their study. Appanah et al. (1986) demonstrated temporal changes in the number of pollen foragers of *Trigona* colonies, and found that some sudden increases in the number of pollen foragers for a few weeks occurred during 13 months. These lines of evidence suggest that such an abrupt increase in pollen diet similarity is rare owing to an occasional and local flowering event.

4.3. Temporally stable breadth of pollen diets

The third result suggests that pollen diet breadth is temporally stable when species richness of flowering plants changes. Eltz et al. (2001) also found that pollen type richness did not change while evenness index slightly increased as species richness of flowering plants increased. Although mechanisms to stabilize diet breadth are unclear, social foraging system can affect diet choice at colony level. *Trigona* species communicate direction of food sources, and recruit foragers to selected resources (Nieh et al., 1999).

This study showed that pollen type richness was highest in *T. melina*, followed by *T. melanocephala* and *T. collina*. Eltz et al. (2001) obtained similar results. These results may be a consequence of both frequent forager returns and abundant pollen foragers in *T. melina* and *T. melanocephala*. Relationship of pollen diet similarity among the three species also agrees between Eltz et al. (2001) and our study. This consistency suggests that preference in pollen diets of each species is stable throughout temporal and spatial variation in floral resources.

ACKNOWLEDGMENTS

We would like to thank H.S. Lee and A.A. Hamid, of the Forest Department, Sarawak, and K. Ogino, of the Shiga Prefectural University for supporting this research project. We are also grateful to anonymous reviewers, D.W. Roubik, N. Osawa, T. Itioka, and S. Sakai for reviewing the manuscript. The study was supported by Grant-in-Aids from the Japan Ministry of Education, Science, and Culture (04041067, 06041013, and 09N1501) and by a JSTC Domestic Research Fellowship for T. Nagamitsu.

Résumé – Activité de butinage et régime pollinique de colonies d'abeilles sans aiguillon à nidification souterraine en réponse à la floraison généralisée à Sarawak, Malaisie. La floraison généralisée est un type de floraison en masse qui se produit simultanément pour la plupart des plantes, à intervalles irréguliers de 2–10 ans dans le sud est asiatique. Dans le nord du Sarawak, une floraison généralisée a eu lieu en 1996 après un intervalle de quatre ans. Plus de 17 % des espèces florales et des individus ont fleuri en 1996, alors que moins de 5 % avaient fleuri en 1994. Le nombre de fleurs sur chaque plante a également augmenté en 1996. Cette différence a fourni l'occasion d'étudier la réponse des abeilles sans aiguillon à cette floraison générale du point de vue du butinage. L'activité de butinage de six colonies et le régime pollinique de trois colonies d'abeilles sans aiguillon à nidification souterraine

(*Trigona* spp.) ont été notés sur trois périodes et comparés entre 1994 et 1996. Parmi les variables de l'activité de butinage (fréquence des retours de butineuses, proportions des butineuses de nectar et des butineuses de pollen), seule la fréquence de retours des butineuses était significativement plus élevée en 1996 qu'en 1994 (Fig. 1). Les trois variables présentaient des différences significatives d'une période à l'autre et d'une colonie à l'autre (Figs. 2 et 3). Parmi les variables du régime pollinique (richesse en types polliniques, indices de diversité et de régularité), aucune ne différait significativement d'une année à l'autre, d'une période à l'autre ou d'une colonie à l'autre, mis à part la richesse en types polliniques qui présentait des différences entre colonies. La similitude du régime pollinique entre colonies ne différait pas significativement entre années mais différait entre périodes et entre paires de colonies (Fig. 4). Ces résultats suggèrent que la réponse des colonies se caractérise par (i) la fréquence des retours des butineuses en réponse à la floraison générale, (ii) les proportions de butineuses de nectar et de pollen et la similitude du régime pollinique répondent plutôt à la fluctuation des ressources qu'aux cycles de floraison généralisée, (iii) l'étendue du régime pollinique est stable dans le temps.

***Trigona* / butinage / floraison généralisée / nectar / régime pollinique / forêt mixte à diptérocarpes de basses terres**

Zusammenfassung – Sammelaktivität und Polleneintrag unterirdisch lebender Völker Stachelloser Bienen als Reaktion auf die Hauptblüte in Sarawak, Malaysia. Die Hauptblüte ist eine Form der Massenblüte, die in unregelmäßigen Abständen von 2–10 Jahren bei den meisten Pflanzenarten in Südostasien gleichzeitig abläuft. 1996 trat im nördlichen Sarawak eine Hauptblüte nach einer 4jährigen Unterbrechung auf. Mehr als 17 % der Pflanzenarten und – individuen blühten 1996, während 1994 weniger als 5 % der Pflanzenarten und – individuen blühten. Auch die Anzahl der Blüten pro Pflanze war 1996 erhöht. Dieser Unterschied bot eine gute Gelegenheit, das Sammelverhalten Stachelloser Bienen als Reaktion auf die Hauptblüte zu untersuchen. Die Sammelaktivität von 6 Völkern und der Polleneintrag von 3 Völkern unterirdisch lebender Stachelloser Bienen (*Trigona* ssp.) während dreier Untersuchungszeiträume wurden zwischen 1994 und 1996 verglichen. Unter den Variablen der Sammelaktivität (Häufigkeit der Rückkehr von Sammelbienen, Anteile nektar- und pollensammelnder Bienen) war es nur die Häufigkeit der Rückkehr von Sammelbienen, die 1996 signifikant höher lag als 1994 (Abb. 1). Die Anteile der Bienen, die mit Nektar zurückkehrten, variierte signifikant zwischen den Untersuchungszeiträumen und alle 3 Variablen variierten zwischen den Völkern (Abb. 2 und 3). Was die Variablen der Vielseitigkeit des Polleneintrags anbelangt (Anzahl der verschiedenen Pollentypen, Diversitäts-Index und Evenness-Index), so variierte keine davon signifikant zwischen den Jahren, den Untersuchungszeiträumen oder den Völkern. Einzige Ausnahme war die Anzahl der verschiedenen Pollentypen, die zwischen den Völkern variierte. Die Ähnlichkeit des Polleneintrags zwischen den Völkern variierte nicht signifikant zwischen den Jahren, obwohl sie zwischen den Untersuchungszeiträumen und zwischen Völker-Paaren (Abb. 4) variierte. Diese Ergebnisse lassen auf folgende Merkmale einer Volksreaktion schließen: (1) Die Häufigkeit der Rückkehr von Sammelbienen erhöht sich in Reaktion auf die Hauptblüte. (2) Die Anteile nektarsammelnder Bienen und die Ähnlichkeit des Polleneintrags sprechen eher auf kürzere Nahrungsquellen-Fluktuationen an als auf die Hauptblühzyklen. (3) Die Vielseitigkeit des Polleneintrags ist zeitlich stabil.

Gemischter Tiefland-Dipterokarpwald / Futtersuche / Allgemeine Blütezeit / Nektar / Pollennahrung / Sarawak / *Trigona*

Appendix. Pollen types utilized by three *Trigona* colonies C (*T. collina*), E (*T. melanocephala*) and F (*T. melina*) in three periods (1: 22–23 June, 2: 10–13 August and 3: 17–19 September) in 1994 and three periods (4: 15–18 May, 5: 4–8 August and 6: 19–23 August) in 1996, and the number of pollen foragers that mainly utilized each pollen type.

		1994 (reduced flowering)									1996 (general flowering)									
ID	Family	C1	C2	C3	E1	E2	E3	F1	F2	F3	C4	C5	C6	E4	E5	E6	F4	F5	F6	Total
A1	Araceae							4	22	10										36
A2	Araceae																	8		8
A3	Araceae														1			4	1	6
A4	Araceae				1															1
A5	Araceae									1										1
B1	Annonaceae				17	12														29
B2	Annonaceae														4	1		1		6
B3	Annonaceae														3					3
B4	Annonaceae																2			2
B5	Annonaceae					2														2
B6	Annonaceae																1			1
B7	Annonaceae																		1	1
B8	Annonaceae									1										1
C1	Euphorbiaceae												5			10			5	20
C2	Euphorbiaceae/ *Drypetes*								8	2										10
C3	Euphorbiaceae/ *Croton*								1											1
D1	Arecaceae				5	1		1												7
D2	Arecaceae/ *Calamus*				1		1	3												5
D3	Arecaceae																	1	2	3
D4	Arecaceae								3											3
D5	Arecaceae																2			2
D6	Arecaceae/ *Calamus*				1															1
D7	Arecaceae/ *Calamus*							1												1
E1	Urticaceae				1	1	2	8	5											17
E2	Urticaceae																1			1
E3	Urticaceae	1																		1
F1	Fabaceae/ *Mimosa*	8	2								5			1						16
F2	Fabaceae		1																	1
G1	Passifloraceae/ *Passiflora*	5	10	1							1									17
H1	Aristolochiaceae													8			1			9
I1	Cucurbitaceae											4								4
I2	Cucurbitaceae	1	1																	2
I3	Cucurbitaceae	2																		2
J1	Plumbaginaceae		2	3							2									7
K1	Cyperaceae	3				1														4
K2	Cyperaceae															2				2

L1	Rubiaceae						2			4										6
M1	Melastomataceae													1						1
M2	Melastomataceae																		1	1
M3	Melastomataceae							1												1
N1	Anacardiaceae				2															2
O1	Loranthaceae						1			1										2
P1	Onagraceae/ *Ludwigia*						2													2
Q1	Poaceae												1							1
Q2	Poaceae					1														1
R1	Ericaceae														1					1
Z01												8								8
Z02							4			3										7
Z03																2		1	2	5
Z04																2			1	3
Z05														2						2
Z06											1			1						2
Z07															2					2
Z08												1	1							2
Z09																			2	2
Z10																			2	2
Z11													2							2
Z12					2															2
Z13						1			1											2
Z14														1						1
Z15																	1			1
Z16																	1			1
Z17														1						1
Z18														1						1
Z19																		1		1
Z20												1								1
Z21																1				1
Z22													1							1
Z23																			1	1
Z24							1													1
Z25		1																		1
Z26		1																		1
Z27								1												1
Z28				1																1
Total		22	16	5	30	19	13	19	40	22	9	14	10	16	11	18	9	16	18	307

REFERENCES

Appanah S. (1985) General flowering in the climax rain forests of South-east Asia, J. Trop. Ecol. 1, 225–240.

Appanah S. (1993) Mass flowering of dipterocarp forests in the aseasonal tropics, J. Biosci. 18, 457–474.

Appanah S., Chan H.T. (1981) Thrips: the pollinators of some dipterocarps, Malaysian Forest. 44, 234–252.

Appanah S., Willemstein S.C., Marshall A.G. (1986) Pollen foraging by two *Trigona* colonies in a Malaysian rain forest, Malayan Nat. J. 39, 177–191.

Ashton P.S., Givinish T.J., Appanah S. (1988) Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of

mast fruiting in the aseasonal tropics, Am. Nat. 132, 44–66.

Eltz T., Bruhl C.A., van der Kaars S., Chey V.K., Linsenmair K.E. (2001) Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest, Insectes Soc. 48, 273–279.

Erdtman G. (1960) The acetolysis method – a revised description, Sven. Bot. Tidskr. 54, 561–564.

Huang T.C. (1972) Pollen flora of Taiwan, National Taiwan University, Botany Department Press, Taipei.

Inoue T., Nakamura K., Salmah S., Abbas I. (1993) Population dynamics of animals in unpredictably-changing tropical environments, J. Biosci. 18, 425–455.

Inoue T., Sakagami S.F., Salmah S., Nukmal N. (1984) Discovery of successful absconding in the stingless bee *Trigona (Tetragonula) laeviceps*, J. Apic. Res. 23, 136–142.

Inoue T., Salmah S., Abbas I., Yusuf E. (1985) Foraging behavior of individual workers and foraging dynamics of colonies of three Sumatran stingless bees, Res. Popul. Ecol. 27, 373–392.

Inoue T., Salmah S., Sakagami S.F. (1996) Individual variations in worker polyethism of the Sumatran stingless bee, *Trigona (Tetragonula) minangkabau* (Apidae, Meliponinae), Jap. J. Entomol. 64, 641–668.

Inoue T., Salmah S., Sakagami S.F., Yamane S., Kato M. (1990) An analysis of anthophilous insects in central Sumatra, in: Sakagami S.F., Ohgushi R., Roubik D.W. (Eds.), Natural history of social wasps and bees in equatorial Sumatra, Hokkaido University Press, Sapporo, pp. 201–218.

Inoue T., Yumoto T., Hamid A.A., Lee H.S., Ogino K. (1995) Construction of a canopy observation system in a tropical rainforest of Sarawak, Selbyana 16, 24–35.

Itioka T., Inoue T., Kaliang H., Kato M., Nagamitsu T., Momose K., Sakai S., Yumoto T., Mohamad S.U., Hamid A.A., Yamane S. (2001) Six-year population fluctuation of the giant honey bee *Apis dorsata* F. (Hymenoptera: Apidae) in a tropical lowland dipterocarp forest in Sarawak, Ann. Entomol. Soc. Am. 94, 545–549.

Michener C.D. (2000) The Bees of the World, The Johns Hopkins University Press, Baltimore.

Momose K., Yumoto T., Nagamitsu T., Kato M., Nagamasu H., Sakai S., Harrison R.D., Hamid A.A., Inoue T. (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest, Am. J. Bot. 85, 1477–1501.

Morisita M. (1959) Measuring of interspecific association and similarity between communities, Mem. Fac. Sci. Kyusyu Univ., Series E (Biology) 3, 65–80.

Nagamitsu T., Inoue T. (1997) Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest, Oecologia 110, 432–439.

Nagamitsu T., Momose K., Inoue T., Roubik D.W. (1999) Preference in flower visits and partitioning in pollen diets of stingless bees in an Asian tropical Rain forest, Res. Popul. Ecol. 41, 195–202.

Nieh J.C., Tautz J., Spaethe J., Bartareau T. (1999) The communication of food location by a primitive stingless bee, *Trigona carbonaria*, Zoology 102, 238–246.

Pielou E.C. (1966) The measurement of diversity in different types of biological collections, J. Theor. Biol. 13, 131–144.

Richlefs R.E., Lau M. (1980) Bias and dispersion of overlap indices: results of some Monte Carlo simulations, Ecology 61, 1019–1024.

Roubik D.W. (1982) Seasonality in colony food storage, brood production and adult survivorship: studies of *Melipona* in tropical forest (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 55, 789–800.

Roubik D.W., Buchmann S.L. (1984) Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest, Oecologia 61, 1–10.

Roubik D.W., Moreno J.E. (1991) Pollen and spores in Barro Colorado Island, Monographs in Systematic Botany from the Missouri Botanical Garden nº 36, 268 p.

Sakagami S.F., Inoue T., Yamane S., Salmah S. (1983) Nest architecture and colony composition of the Sumatran stingless bee *Trigona (Tetragonula) laeviceps*, Kontyu 51, 100–111.

Sakai S. (2001) Phenological diversity in tropical forests, Popul. Ecol. 43, 77–86.

Sakai S., Momose K., Yumoto T., Kato M., Inoue T. (1999a) Beetle pollination of *Shorea parvifolia* (Section *Mutica*, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia, Am. J. Bot. 86, 62–69.

Sakai S., Momose K., Yumoto T., Nagamitsu T., Nagamasu H., Hamid A.A., Nakashizuka T., Inoue T. (1999b) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia, Am. J. Bot. 86, 1414–1436.

Tissot C., Chikhi H., Nayar T.S. (1994) Pollen of wet evergreen forests of the western Ghats, India, Institut Français de Pondichery, Pondichéry (India).

Yasuda M., Matsumoto J., Osada N., Ichikawa S., Kachi S., Tani N., Okuda M., Furukawa T., Nik A.A.R., Manokaran N. (1999) The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula, J. Trop. Ecol. 15, 437–449.