Canopy Foraging by Two Tropical Honeybees: Bee Height Fidelity and Tree Genetic Neighborhoods

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ABSTRACT Honeybees trained to scented sugar solution feeders were monitored along 220 m of canopy walkways and three 50-65 m tree towers using a canopy access system (LHS) in Lambir Hills, Sarawak to study pollination and bee foraging patterns. Feeder presentation was manipulated and included ground level stations to evoke variation in bee search behavior. *Apis koschevnikovi* (*Ak*) and *Apis dorsata* (*Ad*) discovered feeders rapidly and moved 220 m between tree towers in as little as 6 min, recruiting 2-4 thousand bees in response to 1 L artificial nectar. Experienced bees discovered new feeders in less than 5 min within LHS. Height fidelity was 70 % within trees and 55 % between trees for *Ak*, and 60 % for each among *Ad*. Travel between trees tended downward for *Ad* but upward for *Ak*, with no vertical directional preference detected within trees. Increased resource patchiness augmented bee vagility, but not appreciably between trees. Bees visited feeders between tree tops and ground level, some traveling at least 640 m. Thus, genetic neighborhood size of plants they pollinate exceeds 0.3 km².

Key Words: honeybee / *Apis* / foraging / canopy

Honeybees are among the most frequent visitors of flowering trees in southeast Asian forests (Appanah, 1979, 1981, 1987, Inoue *et al.*, 1990, 1993, Salmah *et al.*, 1990). While African honeybees and some native neotropical bees forage both in the canopy and understory (Roubik, 1993a, Nieh and Roubik, in press), others seem restricted primarily to lower strata, and canopy specialists are unknown (Roubik, 1993a, Nagamitsu and Inoue, 1994). Nonetheless, general searching behavior and ultimately the movement patterns of pollinator's foraging in the canopy remain unassessed variables (but see Kevan, 1990, Bawa *et al.*, 1985, review by Roubik, 1989). Recent electrophoretic work (Murawski, 1995) shows that gene flow usually occurs between adjacent trees, as predicted by Frankie *et al.* (1976) but many details of pollinator behavior and patterns of gene flow have not been studied.

In 1993 we completed a canopy access system in the mixed dipterocarp forest of Lambir Hills National Park, Sarawak, to investigate pollination biology (Inoue and Hamid, 1994). This paper reports the inter-tree movement, site constancy, stratum selection behavior and height fidelity of two common honeybees in southeast Asian forests, *Apis koschevnikovi* and *A. dorsata*, trained to artificial nectar feeders distributed within forest canopy. Their performance as social bees recruiting many foragers is used to derive a general model of pollinator behavior using empirical data covering most of the tropical forest canopy.

METHODS AND MATERIALS

The canopy access system in Lambir Hills National Park (LHS) consists of a 220 m of walkways connecting eight trees to two wooden tree towers, built alongside the arboreal endpoints of the system. Tower 2 (T2) is attached to an individual 50 m *Dipterocarpus pachyphyllus* and Tower 1 (T1) is constructed around a 70 m *Dryobalanops lanceolata*. Tower 3 (T3), consisting of four platforms connected by aluminum ladders, is located on an individual *Dryobalanops aromatica* of 55 m height, 70 m SE of T1. Studies were made during April, 1993 and March-April, 1995 using a range of positions accessible by the combined LHS trees, towers and walkways, and also positions near ground level.

Sugar or honey solutions were used to attract foraging honeybees, marked with paint of different colors according to the feeding station where they first arrived. Observations were made for 9 days in 1993 and 14 days in 1995. Foraging performance was analyzed to estimate foraging range and, consequently, the genetic neighborhood of trees pollinated by the honeybees. Further, relatively few competing trees or shrubs were in flower, allowing us to quantify the following aspects of bee foraging behavior and to construct falsifiable hypotheses:

- 1) Forage discovery rate and colony forager recruitment dynamics
- 2) Forager population size
- 3) Intertree movement patterns:
 - a) rate and speed of movement between tree towers
 - b) degree of height fidelity (proportion of re-sighted marked individuals returning to the original level where marked)
 - c) proportion of marked individuals arriving at lower or higher forage sites
 - d) factors promoting inter-tree movement as a function of: i) distance between forage sites; ii) height of forage sites; iii) temporal and spatial pattern of forage presentation
- 4) Intratree movement patterns: degree of height fidelity

Weather conditions were usually still and humid during the morning, with occasional thunderstorms in early afternoon terminating our studies. Observations usually commenced before 0700 and ended by mid afternoon. Air temperatures ranged from 29°C to 33°C during the studies, with a maximum of 40°C recorded in full sunlight at 45 m on T2.

Sugar bait presentation incorporated hand-held spray bottles and saturated sponges in plastic containers. Sugar solutions were made by diluting honey with water in a 1:1 mixture, yielding a solution 40 % sugar by weight, or by mixing table sugar with water, 2:1 by volume, yielding 50 % sugar solutions by weight (measured with a refractometer). Both solutions were flavored with anise extract by 3-5 drops per liter. Used primarily to initiate baiting studies, the hand-held sprayer and honey water were expected to enhance olfactory detection by foraging bees. Several ml of solution were sprayed in a fine mist directly on leaves (see Roubik, 1980). After bees arrived at the honey-water, the sprayer was used to apply bait to light blue or yellow sponge feeders. On following days, sugar water was poured directly onto sponges of 3 cm thickness in plastic containers, and replenished periodically with the sprayer or by pouring, with minimal dispensation of sprayed mist.

A total of 1 liter solution was used for the feeding studies each day. Bait presentation was terminated when foragers had removed the 1 liter of solution, which was dispensed periodically during counts of the foraging bees. In studies of 1993, three to seven individual feeders were used at one time, and during 1995, up to eight feeders were presented simultaneously. Feeder positions and presentation schedules are summarized in Table 1. On walkways, feeders were

Table 1. Feeder presentation and marking schemes of honeybees, *Apis koschevnikovi* (Ak) and *Apis dorsata* (Ad), in a mixed dipterocarp forest at Lambir Hills National Park, Sarawak.

Experiment, # and date	Time and site**	N obs (level)	Hypotheses*	New tags	
				Ak	Ad
in 1993					
1, 17 Apr	0730-1200 T1	1-7	1-3	60	
	0820-1140 T2	2	1-3	121	
2, 18 Apr	0800-1040 T2	4	2-4	293	
	1300-1445 T1	3	2-4	460	
3, 19 Apr	0815-1530 T1	5	2-4	25	108
	0830-1500 T2	5	2-4	49	
4, 20 Apr	0700-1045 T1	4	2-4		700
	0835-1300 T2	7	2-4		
5, 21 Apr	0830-1240 T1	6	2-4		
	0710-1130 T2	6	2-4		
6, 22 Apr	0730-1010 T1	3 (low)	2-4		
	0715-1045 T2	3 (high)	2-4		
7, 23 Apr	0655-1150 T1	6 (high)	2-4		
	0718-1150 T2	6 (low)	2-4		
8, 24 Apr	0648-1338 T1	4 (high)	2-4	50	
	0716-1338 T2	4 (high)	2-4	62	
9, 24 Apr	1515-1655 lab	9	2-4		
10, 25 Apr	0830-0928 T1	2 (low)	2-4		
	0845-1015	2 (low)	2-4		
in 1995					
11, 20 Mar	0725-0940 T2	37	1-3	415	
12, 21 Mar	0957-1348 T1,Ww	4-5	1-4		
	0640-0845 lab	4	2	100	
13, 22 Mar	0708-1105 T2	12 (top,mid)	2,3	464	
	0700-1140 T1,Ww	7	2-4		
14, 23 Mar	1315-1600 lab	2	3	113	
	0650-1202 T2	9	2,3	340	
15, 24 Mar	0643-0907 T1	24	1-4	200	
	1250-1320 lab	3	2		
16, 25 Mar	0720-1055 Ww	3	2,3		
17, 30 Mar	0632-0744 T2	11 (top,mid)	1-3	250	
	0803-1130 Ww	6	1-3		
	1300-1520 lab	2	3	150	
18, 31 Mar	0625-0915 T1	12	1-4		
	0924-1050 T2	8	1-3		
	1146 lab	1	2		
19, 1 Apr	0640-1002 T1	19, 6	2-4		
	0717-1040 Ww	3	2,3		
19, 1 Apr	1100-1142 T2	6, 9	2,3		
20, 2 Apr	0618-0915 T3	33	1-4		
	1030-1049 lab	5	2		
Total no. marked				3152	808

*see text in Methods and Materials.

**T1, T2, T3: Tree tower 1, 2 and 3, respectively, Ww: Walkways between T1 and T2, and lab: the laboratory house.

placed either near the middle of walkways or at the trees between walkways.

In 1993, our experiments tested whether different feeder presentation schedules, in part following nectar secretion patterns noted for tropical trees (Frankie *et al.*, 1976; Frankie and Haber, 1983), affected bee movement patterns. Experiment sequences were as follows: Four

two-day baiting runs at T1 and T2 mimicked flowering trees that 1) produce nectar synchronously, first in the morning, then in the afternoon; 2) produce nectar at different times, one in the morning and one in the afternoon; 3) produce nectar simultaneously, but in different strata (high or low, the 32-45 m levels, or the 3-20 m levels), or 4) produce nectar simultaneously and at the same level, but only at high or low levels. The paired experiments were reciprocal. That is, when asynchronous timing or placement were used, each tower was used once in each configuration. During 1995, studies included observations on bee movement along the walkway, between LHS and T3, and to the superior two platforms of T1, at 45 and 55 m.

Foraging bees at feeders, *Apis koschevnikovi* (*Ak*) or *A. dorsata* (*Ad*) were tagged by painting a patch on the thorax or abdomen. Bees continued imbibing while paint was applied. Tag loss due to messy application or smearing by bees attempting to remove paint was minimal. However, an instance of massive recruitment by *Ad* led to stinging of the observer, halting further work on one day. Bees were marked with a different color—white, yellow, green, pink, fluorescent orange, light blue or red – at forage sites. Color corresponded to feeders at a particular height. At T1, bees were marked at 3 m, 16 m and 33 m above ground level. At T2, bees were marked at 4 m, 20 m, 32 m and 45 m. Bees at ground level were also marked at feeders near the laboratory house, which was 620 m SE of T2 and 400 m SE of T1. For 1993 studies, foragers of *Ak* and *Ad* were tagged at all the indicated levels at T1 and T2, on the thorax or abdomen, respectively. In 1995 no *Ad* were present; *Ak* were tagged at two levels on T2, and at ground level near the laboratory house.

Field data were taken on numbers of marked and unmarked foragers at individual feeding stations by repeated censusing, in which an observer moved among feeders, usually spending the same amount of time at each. Several counts at each feeder during a day were usually made, but census intervals varied, depending on the length of the aerial transect and number of total census counts (Table 1). Foragers were generally tagged in batches of 20 or 100 at a particular level. Unmarked foragers were painted until several hundred were marked (Table 1).

RESULTS

Discovery and Recruitment

Upon initial bait presentations in 1993 and 1995 at canopy level, feeders were discovered by foraging *Ak* in less than 5 minutes. After four days when no baits had been present, an unmarked *Ak* carrying a small pollen load (no flowers were near the tree-tower) arrived almost instantly at a bait placed at 45 m at 0635. Five foragers arrived within 2 min and departed in less than 15 seconds. The first marked bees, originally from 20 m and 45 m, arrived within 6 min of bait presentation. Foragers of *Ad* found feeders after two days of foraging by *Ak*, then visited all feeders. Apparently from a single colony, suggested by lack of aggression between foragers, the estimated number of *Ad* matched or exceeded that of *Ak* from multiple colonies (Table 2). Intertree movement of marked foragers, covering 220 meters between T1 and T2, occurred in as little as 10 min for *Ak* and 6 min for *Ad* (see following section). Once foraging colonies were trained to baits, new baits in different positions were rapidly discovered.

On the final experiment in 1995, baits positioned in T3 before dawn (approximately 0610) attracted bees at 60 m by 0618. The first marked bees were spotted on the highest and next highest levels at 0646. Each marked bee had been marked at 45 m on T2. Early arrivals flew into the tree upwind, apparently just above the canopy. Later, bees flew back and forth along the tree trunk, while flying upward or downward. The lower two levels of T3 were visited by

Table 2. Mark-recapture estimates of honeybee forager populations (N: mean, and 95 % of Confidence Limit) at Lambir Hills National Park, Sarawak.

Date, species	Observation post	N	95 % C. I.
<i>Apis koschevnikovi</i>			
17 Apr '93	T1	455	103
18 Apr '93	T1	1796	265
	T2	1676	189
19 Apr '93	T1	2313	300
	T2	2793	447
20 Apr '93	T2	1701	165
21 Apr '93	T1	2385	518
	T2	1523	265
22 Apr '93	T1	3042	1261
	T2	1325	164
23 Apr '93	T1	3619	1819
	T2	2516	814
24 Apr '93	T1	3668	2045
	T2	2439	377
25 Apr '93	T1	3249	1333
	T2	1908	531
20 Mar '95	T2	817	158
	Ww	1453	439
	T2	1473	534
	Ww+T1	1739	632
	Ww+T1	1858	651
	Ww only	1686	703
21 Mar '95	lab	211	49
	lab	282	84
	T2	2092	487
	T2	4226	447
	T2	3465	225
22 Mar '95	Ww-from T2	11655	2325
	Ww-from lab	1560	214
	Ww-T2 top	4226	447
	Ww-T2 mid	8532	26
23 Mar '95	T2	6691	621
24 Mar '95	T1	11545	870
	T2	6045	476
	lab	630	101
25 Mar '95	Ww-T2 top	7588	1501
	Ww-T2 mid	6299	1438
	Ww-lab	8682	3395
30 Mar '95	T2	10064	1689
	Ww	9761	935
31 Mar '95	T1	17518	2034
	T2	15381	2803
	lab	2678	528
1 Apr '95	T1	33379	4830
	T2	10840	2440
	Ww	25597	4278
2 Apr '95	lab	1986	450
	T3	45217	5907
<i>Apis dorsata</i>			
20 Apr '93	T1	2310	283
20 Apr '93	T2	3165	477
21 Apr '93	T1	3871	383
	T2	3352	288
22 Apr '93	T1	4435	414
	T2	2648	638
23 Apr '93	T1	4758	308
	T2	2543	629
24 Apr '93	T1	4238	615
	T2	3126	474
25 Apr '93	T1	1823	262
	T2	3234	378

Table 3. Within-tree height fidelity, from re-sightings of marked *Apis koschevnikovi* and *Apis dorsata* feeding at tree-towers (T1, T2).

Date, species	Level Re-Sighted	Level High	Where Middle	Marked* Low	χ^2 , p	Avg.** Fidelity(%)
<i>Apis koschevnikovi</i>						
18 Apr '93	same	207	123	90	1.15, 0.28**	94
	different	10	14	2		
20-21 Apr '93	same	127	40	34	5.87, 0.05	87
	different	11	9	8		
22-23 Apr '93	same	40	10	14	4.8, 0.09	41
	different	49	7	32		
24-25 Apr '93	same	54	6	9	41.2, 0.001	58
	different	8	13	25		
21 Mar '95	same	113	195		17.0, 0.0001	76
	different		55	35		
23 Mar '95	same	152	67		18.4, 0.0001	76
	different		21	34		
24 Mar '93	same	185	119		2.1, 0.20	69
	different		25	25		
30 Mar '93	same	51	39		1.3, 0.36	79
	different		10	13		
31 Mar '93	same	42	24		0.66, 0.57	72
	different		13	11		
1 Apr '93	same	27	5		1.89, 0.29	49
	different		18	8		
<i>Apis dorsata</i>						
20-21 Apr '93	same	294	91	57	31.3, 0.0001	64
	different	231	49	5		
22-23 Apr '93	same	201	25	6	1.8, 0.40**	56
	different	138	25	3		
24-25 Apr '93	same	141	14	-	6.08, 0.01**	45
	different	111	23	3		

* levels 32 m and 45 m on T2 were pooled.

**2×2 contingency tables were used because of low expected cell counts of 2×3 tables (low and middle were pooled), average fidelity also pooled low and middle.

Ak after approximately 0710. The first marked bee from ground level arrived at the 60 m platform of T3 at 0658, and the first marked bees from the 20 m platform on T2 at 0656. Bees of the lab predominated, to which 59 % of the 224 marked bees sighted on T3 belonged. Only 5 % of the bees seen at T3 were marked, approximately one-half to one-third the ratio of marked bees seen on T1, T2 or the walkway (see below).

Discovery was not rapid for feeders near ground level when bees had been trained only to middle and upper canopy. Two days of feeder placement at 2 m on four trees of the walkways between T1 and T2 produced no *Ak*. In 1995, only 44 of 449 total bees (10 %) arriving at feeders near ground (1.5 m) at T1 and T2 had been marked, compared to 16 % of 26,480 bees at feeders on walkways and tree towers. This difference in proportion was significant by a contingency table test of association ($\chi^2 = 6.57$, $p = 0.01$), thus suggesting bees marked in the canopy were less likely to encounter feeders near ground level. On 31 March, 1995, high platforms at 45 m and 55 m on T1 received 5 of 59 bees (15 %) tagged at ground level at the lab, while only 1 of 100 bees marked at T2 at 45 m came to the feeders on the lowest level (see Fig. 2). In contrast, tests of association indicate bees were no more likely to forage along walkways whether they had been previously trained to feeders at ground level or in the canopy ($p = 0.6$, Table 3). Walkways had higher representation from bees marked at the lab on 22 March, then relatively few of these, and predominantly bees from 20 m on T2 during

Fig. 1. Logistic increase in the number of foragers of *Apis koschevnikovi* on feeders during the first morning of baiting (1995).

March 30 (Table 3).

Recruitment dynamics of *Ak* were followed closely on one occasion after initial feeder discovery on the first day of studies in 1995 (Fig. 1). Their increase on feeders was logistic. The maximum bees found at feeders were 321, while the total numbers of foragers reached approximately 1-2 thousand (Table 2).

Forager Population Size

At least three colonies of *Ak* foraged at feeders, indicated by departure of bees in different directions after feeding, and by brief skirmishes between foragers in both years, even when baits were not near depletion. Ratios of marked to unmarked foragers allow a single-recapture estimate of forager population size, N , based on the Peterson method (Southwood, 1978, Table 2). Given that tag loss occurred after a few days (foragers were noticeably more often hairless on the thorax a few days after several hundred were painted – paint was likely chewed away by nestmates) we believe the most accurate estimates follow closely the marking of many bees. Estimates therefore did not include several observations after 25 March which would inflate population estimates. The selected data suggest that after two days, recruitment to baits in the canopy involved from roughly 1-12,000 workers of *Ak* in 1995, or an average of 4000 workers bracketed by 95% confidence intervals (3280-4904) and 1993 (1613-2938, average with 95 % C. I. s). A single colony of *Ad* had forager numbers averaging 3155 (2757-3552, see Table 2).

Intra-tree movement patterns

Within tree-towers where bees were marked, *Ak* were slightly more constant to feeders than were *Ad*. Notable exceptions occurred in experiments using feeders in only some strata but not others (the 'high-low' and 'high-high', 'low-low' studies of 1993, Table 3, also see Methods). After the aforementioned manipulations in 1993, returns to the same level were seen only in 41 % and 52 % of re-sighted *Ak*, similar to the 41-56 % height fidelity among *Ad* at the same time. Although *Ad* also responded with more vagility, changes in movement patterns by *Ad* seemed less affected by the experiments. The average performance of *Ak* was virtually identical in 1993 and 1995, with a mean of 70 % foragers displaying height fidelity. *Ad* displayed mean height fidelity of 55 %.

A grand average of 70 % (SE = 5.2 %) the 2267 marked *Ak* and 55 % (SE = 5.5 %) *Ad*

Table 4. Between-tree height fidelity from re-sightings of marked *Apis koschevnikovi* and *Apis dorsata* feeding at tree-towers (T1, T2).

Date, species	Level Where Re-Sighted	Level Where Marked High	Low	χ^2 , p	Average Fidelity(%)
<i>Apis koschevnikovi</i>					
24 Mar '95	Same	65	39	10.9, 0.001	59
	Different	26	43		
31 Mar '95	Same	88	10	87.2, 0.0001	52
	Different	12	56		
1993 (total)	Same	27	16	0.2, 0.83	55
	Different	25	12		
<i>Apis dorsata</i>					
1993 (total)	Same	150	133	40.9, 0.0001	60
	Different	187	47		

observed on tree towers were later sighted at the height they had been marked (Table 3). Of 970 re-sighted *Ak* in 1993, 30 % had changed level, whereas of 1419 re-sighted *Ad*, 45 % had shifted their foraging stratum (Table 4). Further comparisons were made to determine whether vagility and height fidelity were related to the stratum of marking, given as results of χ^2 contingency tests in Table 4. These evaluate movement patterns on 6 days for *Ad* and 13 days for *Ak*. Slightly more vagility related to level was found among *Ad* than *Ak*. The latter more often tended toward vagility among foragers at lower levels. However, of 13 tests, only 6 showed a significant difference in vagility related to height, and bees marked both at higher and lower levels showed more vagility on one occasion or more for each bee species.

Inter-tree Movement Patterns

Bees moving between tree-towers appeared less constant in foraging height than did bees foraging within trees. Furthermore, although height fidelity was similar between *Ad* (60 %) and *Ak* (55 % in both years), vagility related to height differed for these honeybee species (Table 4).

We observed 901 marked bees that moved between towers 1-3 and along canopy walkways. The two most widely separated observations were the laboratory site and the 45 m platform of T2, 640 m distant along the ground. A total of 227 marked *Ak* from the lab (ground level) were seen at the uppermost platforms of T1 (see Fig. 2) and T3, while only 2 arrived at the top of T2. In 1993 a total of 24 *Ak* marked at the top of T2 or T1 were observed at ground level at the lab. One had been marked at 45 m less than 2 h before it was re-sighted at the lab. During the 1995 studies, only 1 forager marked at T2-20 m, was recorded at the lab.

Did bees more often move up or down when flying between tree towers? Tests of association between height at marking and extent of vagility were significant in 3 of 4 cases, covering 8 days for *Ak* and 6 days for *Ad* (Table 4). Bees of upper levels changed height relatively more often among *Ad*, and bees of lower levels showed less height fidelity for *Ak*. In 1993, daily movements between T1 and T2 showed *Ak* had probabilities of changing foraging level that ranged from 0.29 to 1.00 ($N = 8$ days, 103 re-sightings) using 4 feeder presentation designs and marked bees from three or four levels on T1 and T2 (see Methods). In 1995 only bees on T2 were marked, and only at two levels, top and mid canopy (45 and 20 m). Of 335 re-sighted bees on T1 during this year, during March 24 and March 31 (Fig. 2), 40 % and 60 %, respectively, were at different levels than those at which they were marked. Data taken at individual levels, rather than pooled totals, are appropriate to test whether bees in the

Fig. 2. Height fidelity, expressed as proportions of each height group from bees trained to feeders and marked at T2, then re-sighted on T1 at platforms of five levels the following day (31 March, 1995). Proportions are standardized transformations that correct for differences among the numbers of individuals marked, and marked individuals re-sighted, at each level.

upper or lower stratum were more likely to change level when moving between trees (Table 4). Both days in 1995 showed significant association between vagility and original level ($p < 0.001$), with 51-86 % of *Ak* from 20 m changing level, compared to 12-29 % of bees from 45 m. In contrast, in 1993 *Ak* showed no significant differences, with 48 % of bees marked at 32 to 45 m changing to lower feeders, and 43 % of bees marked at 3 to 20 m moving to higher feeders between trees. Among 517 *Ad* scored for movement between trees, 36 % foraged at the same level where they first were marked, although 55 % were at the same level if upper and lower levels were placed in only two categories, as for *Ak* in 1993. A significant association was found between level and vagility (Table 4), with changes occurring in 79 % of *Ad* marked at higher feeders, compared to 26 % among those from lower levels.

Bees arriving at canopy walkways came from all feeders used to mark bees. Walkways between trees were at a similar height to feeders on T1 at 16 m, with the exception of the first walkway after T2, at 25 m. On the three days walkways were monitored, three different results were obtained (Table 5). On March 22, bees from the laboratory appeared significantly more often than bees from T2. On 25 March, bees from 20 or 45 m on T2 were no different in relative frequency from those of the laboratory. On 30 March, bees foraging on the walkway were relatively more often those from T2 at 20 m. In addition, on 22 March the walkway closest to T1 had the highest proportion of foragers marked at 45 m on T2, and walkway 2 had high proportions of foragers from the lab. During other days there was little difference in distribution of foragers from feeding stations among the walkways, although bees from the lab were absent on the four walkways most distant from it (Tables 3, 5).

Table 5. Canopy walkway re-sightings of marked *Apis koschevnikovi* (1995 only).

Date	Total Marked or re-sighted	Level where marked			χ^2 , p
		lab (ground)	20 m	45 m	
22 Mar	re-sighted	47	34	68	107, 0.0001
	marked	479	300	100	
25 Mar	re-sighted	79	60	23	0.92, 0.63
	marked	879	570	219	
30 Mar	re-sighted	99	144	5	58, 0.0001
	marked	1029	670	219	

Table 6. Total numbers of foragers re-sighted on original tree towers and on different tree towers, and estimated proportion of movements between tree towers (T1, T2), in 1993.

Date, species	Total re-sighted	Total re-sighted from other tree	% movement between trees
<i>Apis koschevnikovi</i>			
18 Apr	102	17	17
19 Apr	120	3	4
	89	5	7
20 Apr	149	6	4
21 Apr	46	1	2
	44	2	5
22 Apr	15	11	73
	63	1	2
23 Apr	11	0	0
	22	2	9
24 Apr	9	0	0
	88	0	0
25 Apr	15	0	0
	21	6	29
<i>Apis dorsata</i>			
20 Apr	129	36	28
	133	46	35
21 Apr	127	58	46
	222	1	<1
22 Apr	74	33	31
	130	36	28
23 Apr	143	20	14
	144	44	31
24 Apr	116	6	5
	102	54	53
25 Apr	46	10	22
	145	47	32

Experiments that varied the timing and position of bait presentation at T1 and T2 during 1993 produced no large changes in inter-tree vagility by bees. To estimate the rate of bee movement between tree towers, the proportion marked at another tower was computed for all the marked bee sightings on individual days, and at each tower (Table 6). Fifty-four re-sighting were made of *Ak*, and 387 of *Ad*. For *Ak* the proportions were lower than for *Ad* (grand means: 11 %, N = 15; 30 %, N = 13, respectively). During the pre-experimental period, vagility ranged from 4 % to 17 % for *Ak*, compared to 1 % to 73 % during subsequent days. Rates of inter-tree movement, from re-sightings of marked *Ad*, ranged from 28 % to 35 % before the experiments, and 5 % to 65 % afterward.

Genetic Neighborhood Size

Bee movement during searching and foraging was rapid within the study area, so that dispersal of viable pollen would presumably occur. The maximum distance a bee traveled between forage sites was about 640 m. Because marked bees foraged over all heights at LHS, their foraging would allow pollen exchange between all plants within an area of at least 640 m in diameter, which is 0.32 km².

DISCUSSION

Bee movement between trees was markedly less influenced by past foraging experience than

was movement within trees. Height fidelity was greater for both bee species within tree towers, compared to between them. Through varied feeder presentation schedules, movement of *Apis koschevnikovi* (*Ak*) between trees separated by 220 m averaged approximately 11 %, while that for *Apis dorsata* (*Ad*) was 30 % of re-sighted marked bees. Intratree vagility by *Ak* appeared to increase when feeder presentation was varied. However, we did not obtain clear evidence for more frequent inter-tree movement when our baiting plan mimicked early and late nectar production by trees, or productive flowers in only some strata of those where bees had foraged previously. Notable variation existed in proportions of bees moving between trees during the 6-day experimental period (Table 6). Neither *Apis* was markedly constant in foraging height, with 70 % intra-tree height fidelity found for *Ak* in both years, compared to 60 % for *Ad*. The latter more readily moved downward over the 220 m between towers, while *Ak* moved upward (see Fig. 2). The probability of changing heights for *Ak* ranged from 0.29 to 1.00 (average 0.58) over 6 periods (10 days). Probabilities of height shifts were similar and ranged from 0.61 to 0.67 in three study periods and six days for *Ad*.

Considering genetic outcrossing, we suggest the ideal distance between individual trees would be that where the probability of a pollinator moving up or down was equal to their probability of moving horizontally. If bees were more inclined to move horizontally, they would skip most flowers of individual trees, and if solely inclined to move vertically, they would not effect outcrossing. The best outcrossing service would be given by foragers that move both up and down trees, and between them. Honeybees were such pollinators. In response to the harvest of one liter of nectar, roughly 3000 bees were mobilized as foragers and potential pollinators, albeit to an artificially compact source of food. In the forest canopy, each searching and foraging bee would visit several dozen to a few hundred flowers after having been recruited to a rewarding nectar source, and thus range over an area of at least a third of a square kilometer. Given these calculations, successful outcrossing seems likely to result from visitation by these honeybees in normal settings, in which one liter of nectar is the standing crop of flowering trees. (A hundred thousand small flowers, each having 10 microliters of nectar, would provide such a resource, see Roubik, 1989, 1993b).

Apis were neither infrequent canopy foragers nor unable to find and then recruit nestmates to feeding sites high in the canopy, among large, emergent trees. Furthermore, in contrast to a few canopy foraging bees or those observed moving between plants (Kevan, 1990; Roubik, 1993a), *Apis* are not particularly stratum constant. Our quantitative treatment is the first given for individual canopy foragers, thus comparative data are not available for other species.

We expect bees to encounter resources by first searching areas where they previously foraged successfully. As demonstrated for several tropical bees, the acuity of bee memory and performance in three dimensions is formidable (Roubik, 1989). Although we studied honeybees, which have an intranidal system for exchange of information, the mechanism of repeated visits to a species in flower, until its resources are depleted at the patch level, should be the same as that of other bees. For all social bees sharing a nest, memory of forage odor should trigger searching behavior in response to a particular incoming resource. Our initial hypotheses to test were that bees either 'scattered', going in all directions and to any level, or that they were guided, either by landmark shapes, colors, odors, or perhaps merely by gravity (see Kevan, 1990) to seek a resource. Our early hypothesis that bees searched visually or in some other manner for a second tree tower after having found food on the first tower was not supported by results with the canopy walkways or T3, all of which were found within minutes. Bees readily found resources in novel places as well as at all points within the LHS, with the exception of resources at ground level when previous foraging experience was in the canopy.

In tall tropical forest such as Lambir Hills mixed dipterocarp forest the honeybees foraged from canopy to ground level, but bees were more likely to discover resources in or near the upper canopy or boundary layer. Location of sugar solutions might be aided by more rapid evaporation of liquids and odors in the upper canopy, and location by color would be facilitated in exposed flowers of the canopy. These hypotheses to be tested would help explain the extraordinary ability of honeybees to exploit canopy resources.

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REFERENCES

- Appanah, S. 1979. The ecology of insect pollination of some tropical rain forest trees. Ph. D. Thesis, University of Malaya, Kuala Lumpur. 213 pp.
- . 1981. Pollination in Malaysian primary forests. *Malaysian Forester* **44**: 37-42.
- . 1987. Insect pollination and the diversity of dipterocarps. In: Kostermans, A. J. G. H. (ed.), *Proceedings of the Third Roundtable Conference on Dipterocarps*, 277-291. UNESCO, Jakarta, Java.
- . 1990. Plant-pollinator in Malaysian rain forests. In: Bawa, K. S. & Hadley, M. (eds.), *Reproductive Ecology of Tropical Forest Plants*, 85-102. Unesco, Paris and The Parthenon Publishing Group, Lancs, U. K.
- Bawa, K. S., Bullock, S. H., Perry, D. R., Coville R. E. & Grayum, M. H. 1985. Reproductive biology of lowland rain forest trees II. Pollination systems. *Amer. J. Botany* **72**:346-356.
- Frankie, G. W. & Haber, W. A. 1983. Why bees move among mass-flowering neotropical trees. In: Jones, C. E. & Little, R. J. (eds.), *Handbook of Experimental Pollination Biology*, 360-372. Van Nostrand Reinhold, New York.
- , Opler, P. A. & Bawa, K. S. 1976. Foraging behavior of solitary bees: Implications for outcrossing of a neotropical forest tree species. *J. Ecol.* **64**:1049-1057.
- 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*, 175-200. Hokkaido University Press, Sapporo.
- & Hamid, A. A. 1994. *Plant Reproductive Systems and Animal Seasonal Dynamics - Long-term Study of Dipterocarp Forests in Sarawak*. Center for Ecological Research, Kyoto University, Otsu.
- , Nakamura, K., Salmah, S. & Abbas, I. 1993. Population dynamics of animals in unpredictably-changing tropical environments. *Journal of Biosciences* **18**: 425-455.
- Kevan, P. G. 1990. How large bees, *Bombus* and *Xylocopa* (Apoidea, Hymenoptera) forage on trees: optimality and patterns of movement in temperate and tropical climates. *Ethology, Ecology and Evolution* **2**:233-242.
- Murawski, D. A. 1995. Reproductive biology and genetics of tropical trees from a canopy perspective. In: Lowman, M. D. & Nadkarni, N. M. (eds.), *Forest Canopies*, 457-493. Academic Press, San Diego, California.
- Nagamitsu, T. & Inoue, T. 1994. Flower-visiting insects collected in lowland dipterocarp forests in Lambir Hills National Park, Sarawak. In: Inoue, T. & Hamid, A. A. (eds.), *Plant*

- Reproductive Systems and Animal Seasonal Dynamics - Long-term Study of Dipterocarp Forests in Sarawak*, 142-150. Center for Ecological Research, Kyoto University, Otsu.
- Nieh, J. & Roubik, D. W. in press. Food recruitment in a stingless bee, *Melipona panamica*: communicating location without a scent trail. *Behavioral Ecology and Sociobiology*.
- Roubik, D. W. 1980. Foraging behavior of competing Africanized honey bees and stingless bees. *Ecology* **61**:836-845.
- . 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.
- . 1993a. Tropical foragers in the canopy and understory: field data and theory for stratum "preferences". *J. Insect Behavior* **6**: 659-673.
- . 1993b. Direct costs of forest reproduction, bee-cycling and the efficiency of pollination modes. *J. Bioscience* **18**: 537-552.
- Salmah, S., Inoue, T. & Sakagami, S. F. 1990. An analysis of apid bee richness (Apidae) in central Sumatra. In: Sakagami, S. F. Ohgushi, R. & Roubik, D. W. (eds), *Natural History of Social Wasps and Bees in Equatorial Sumatra*, 139-174. Hokkaido University Press, Sapporo.
- Southwood, T. R. E. 1978. *Ecological Methods* (2nd edition). Chapman and Hall, London.

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D. W. ROUBIK, 井上民二, A. A. HAMID 2種のミツバチによる熱帯雨林の林冠での採餌：ミツバチの採餌高度に対する固執性と樹木の遺伝子交流範囲

サラワク州ランビル国立公園内に建設された林冠観測システムを利用して、ミツバチの林冠での採餌行動を人工給餌器を用いて調査した。給餌器は地上から林冠上部の間のさまざまな高さに設置し、ミツバチの給餌器間の移動をマーキングによって追跡した。ボルネオミツバチ *Apis koschevnikovi* とオオミツバチ *Apis dorsata* の偵察係は約 220 m はなれて新たに設置された給餌器を6分以内に発見し、そこへ、同じ巣に属する運搬係の働きバチ数千頭を2日以内に動員した。同じ木に反復して訪問する場合、同じ高さにやってくる割合は7割と高かった。同じ高度に訪問しない場合、上下ともに訪問が起こった。別の木に新たに訪問する場合には、この割合は55から60%に低下した。同じ高度を再訪問しない場合、オオミツバチは下方向に、ボルネオミツバチは上方向に訪問がシフトする傾向が強かった。最高 640 m 離れた地点でマーキングされた個体が再捕されており、ミツバチによる遺伝子交流範囲は 0.3 km² 以上であった。この調査から、地上から 70 m 以上に渡って分布する熱帯雨林の林冠内をミツバチは迅速に移動することができ、どの層の花をも利用していることが判明した。