Journal of Apicultural Research 44(4): 180–189 (2005)

ORIGINAL ARTICLE

Periodic mass flights of the giant honey bee *Apis dorsata* in successive days at two nesting sites in different environmental conditions

JERZY WOYKE,[1]* JERZY WILDE,[2] CHANDRASHEKHARA C REDDY[3] AND NARAYANAPPA NAGARAJA[3]

[1]Apicultural Division, Agricultural University, Warsaw, Poland

[2]Apicultural Division, Warmia-Mazury University, Olsztyn, Poland

[3]Zoology Department, Bangalore University, Bangalore, India

Received 1 July 2005, accepted subject to revision 25 August 2005, accepted for publication 14 October 2005

SUMMARY

The investigations were conducted at Bangalore, India. A total of 627 periodic mass flights (PMFs) were observed during 10 successive days from 26 colonies of *Apis dorsata* at a polytechnic building site and 82 colonies at a banyan tree site at the Agricultural University 15 km away. PMF activities performed by particular *A. dorsata* populations were similar in successive days at a particular site. However, at the polytechnic site, where favourable environmental conditions prevailed, 84.3% of colonies performed 2.3 PMFs per colony per day, while at the banyan tree site, with less favourable conditions, only 11.3% of colonies performed 0.11 flights. We suggest that PMF activities depend in part upon the amount of unsealed brood. Individual colonies performed 0–5 PMFs in successive days. Low numbers of 1–2 PMF per day were preceded by high numbers of 4–5 flights the following day. Similarly, PMFs of low intensity were followed by flights of high intensity. However, two- or three-day cycles of similar activities were also observed. Surprisingly, no correlation was found between the sizes of the combs and the number and intensity of PMFs. We explain this by the fact that a similar amount of unsealed brood was present in combs of different sizes.

Keywords: *Apis dorsata*, periodic mass flights, India

INTRODUCTION

Most honey produced in India (about 70–80%) and some other Asian countries is obtained from the giant honey bee, *Apis dorsata*. Many biological phenomena of these bees remain unknown. Investigations on nesting behaviour at the site of the present studies were conducted by Reddy (1983), Reddy & Reddy (1987) and Venkatesh & Reddy (1989).

Colonies of *A. dorsata* perform varying numbers of short, daily periodic mass flights (PMFs) ranging in number from zero to six (Woyke *et al.*, 2005). The flights look like swarming. PMFs apparently play a role in cleansing and orientation flights of young worker bees (Woyke *et al.*, 2003). However, the role of PMFs in nesting biology and behaviour as well as its ecobehavioural significance remains unclear. Therefore it is important to learn more about this phenomenon.

Earlier descriptions of PMFs were concerned with defecation, calling the phenomenon 'yellow rain' (Ashton *et al.*, 1983; Meddox, 1984; Seeley *et al.*, 1985; Mardan & Kevan, 1989). Detailed observations of one PMF performed by *A. dorsata* were reported by Kastberger *et al.* (1996). According to Muthuraman & Srinivasan (2002), the comb became partially exposed during PMFs. Woyke *et al.* (2005) found that worker bees perform mass flights at the time of dusk flights of drones.

Woyke *et al.* (2003) observed variation in the performance of PMFs of *A. laboriosa* made in successive days. Detailed studies of PMF activities performed by *A. dorsata* colonies at weekly intervals over three months showed that 56–100% of colonies performed PMFs per day; particular colonies made zero to six PMFs per day, and the frequency of the number of PMFs over the day had unimodal or bimodal distributions (Woyke *et al.*, 2004). PMF activities differed significantly according to season. However, it was difficult to determine whether variations were due to changing environmental conditions, changed status of the colonies or other unexplained biological variations. Variation in intensity of PMFs has not been investigated until now.

In the present study we seek to explain the degree to which variation in PMF occurrence and intensity can be explained by environmental conditions. To achieve this, we observed PMF activities of *A. dorsata* colonies over 10 successive days. We assumed that the environmental conditions and status of colonies were similar in successive days within a site during the short observation period. The key question was whether PMF activities differ significantly under similar environmental conditions. We observed two *A. dorsata* populations at two nesting sites under different environmental conditions. This should confirm the influence of environmental conditions on the variation of PMFs activities. Below, we first describe PMF activities of the two *A. dorsata* populations at two nesting sites. Next, we analyse PMF activities of individual colonies.

MATERIALS AND METHODS

The investigations were conducted in Bangalore, India, over a 10-day period. Colonies of *A. dorsata* were observed at two nesting sites, one at the polytechnic building in the centre of the city (from 3 to 12 March) and the other on a banyan tree (*Ficus bengalensis*) at the campus of the Agricultural University (from 4 to 13 March), 15 km from the first site. The availability of food resources at the two sites was determined by counting the number of foragers returning to two colonies of similar size (one at each site) for 5 min, hourly from 09:00 to 18:00 h for 3 days.

*Corresponding author: woyke@alpha.sggw.waw.pl

Altogether, 627 PMFs performed by 108 *A. dorsata* colonies were examined in detail. Of those colonies, 21 to 26 were at the polytechnic site and 58 to 82 on the banyan tree. The last higher number of colonies (82) was observed from the fourth day of observation. The colonies at the polytechnic site were observed from a distance of 1.5 m and those on the banyan tree from a distance of 8 to 10 m. Each test colony was marked with a distinctive number.

The condition of the bee colonies at the polytechnic building were examined on 10 March. Bees of 12 accessible colonies were smoked out and the comb size including the quantity of unsealed and sealed brood and its arrangement determined. We had no direct access to the colonies at the banyan tree.

All colonies were observed daily from 08:00 to 19:00 h. The time of beginning and end of PMF activity was recorded. Starting from 6 March, the intensity of PMF activity was examined at the polytechnic site. The intensity was classified according to a 5-grade subjective scale. Grades one to five were characterized by an average number of 6 ± 1.7 (n = 20), 13 ± 1.8 (10), 23 ± 1.9 (20), 33 ± 3.4 (10) and 44 ± 3.8 (10) flying worker bees, respectively, visible near the nest, inside a video frame of 50 × 40 cm. Ambient temperature was measured with an electronic Oregon scientific thermometer placed 1.5 m above the ground under the shade of the polytechnic building and banyan tree.

Statistical analysis

Arcsine transformation was applied to percentages. ANOVA was used to compare variances. Significant differences between particular means were detected by LSD or Duncan's multiple range tests. The t test was applied to determine significant differences between two means. The χ^2 test was used for frequency distribution and comparison of PMFs (Sokal & Rohlf, 2000). In a few cases where the data were fewer than five, exact P values (Ex) instead of χ^2 were computed using R × 2 contingency tables (Mehta & Patel, 2002). Calculations concerning time were made in minutes, but the results are presented in hours and minutes. Statistical tests were made with STATGRAPHICS or STATXACT software packages.

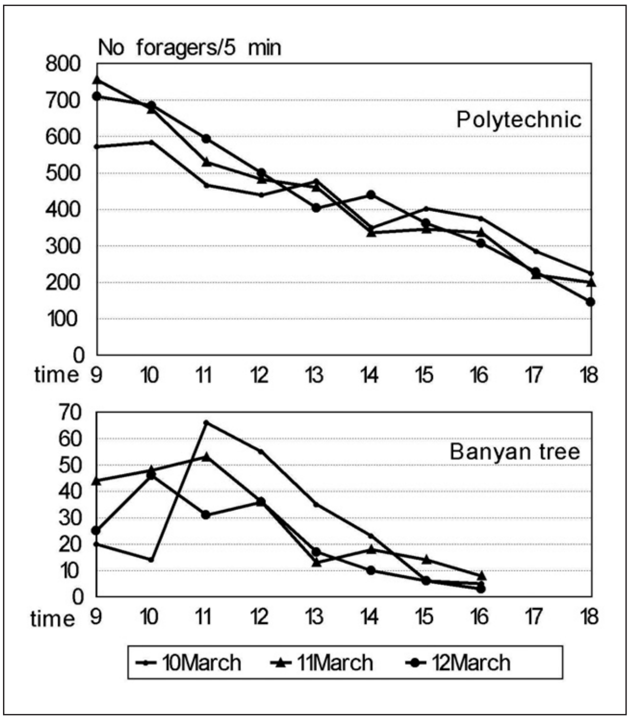

FIG. 1. Foraging activity of *Apis dorsata* worker bees at polytechnic site and banyan tree during three days. Data were collected from 09:00 h to 18:00 h.

RESULTS

Bee flora and food availability at nesting sites

At time of observation many plants were in bloom in the parks, gardens and street avenues near the polytechnic site, particularly *Ailantus excelsia*, *Azadrichta indica*, *Bombax* sp., *Cassia fistula*, *Ceiba pentandra*, *Jacaranda mimosifolia* and *Mangifera indica*. In contrast, the banyan tree site at the Agriculture University was characterized by harvested fields with scattered flowering trees of *Azadrichta indica, Mangifera indica* and *Eucalyptus* sp.

TABLE 1. Characteristics of periodic mass flights (PMFs) performed by *Apis dorsata* worker bees at the polytechnic site.

Date	March 3	4	5	6	7	8	9	10	11	12	Mean	P* χ^2
Temp. avg °C	29.4	28.5	29.0	29.0	28.3	28.2	27.6	28.0	29.7	29.8	28.8	
No. colonies	21	22	23	23	24	24	24	25	25	26	24	
% colonies making PMFs	88	91	87	91	88	75	75	88	82	78	84.3	0.99
No. PMFs	38	47	50	49	59	64	68	60	54	53	54.2	0.87
No. PMFs/col.	1.8	2.1	2.2	2.1	2.5	2.7	2.8	2.4	2.2	2.0	2.3	
No. PMFs/col. making flights	2.1	2.4	2.5	2.3	2.8	3.6	3.8	2.7	2.5	2 9	2.8	
Percentage of colonies performing successive PMFs in ratio to all observed nests												
2nd PMF	57	55	65	57	62	58	63	68	52	58	59.5	0.99
3rd PMF	38	46	30	39	50	54	54	56	48	39	45.4	0.96
4th PMF		23	22	26	38	46	46	28	20	32	31.2	0.83
5th PMF			13		8	21	33		8	8	15.2	
6th PMFs						8	13				10.5	

*P = probability of the χ^2 test for equal frequency distribution of the character in 10 successive days (P > 0.05 indicates similar distribution).
Underlined = for statistical test of equal frequency the no. PMFs in successive days was fitted to the same mean no. of 24 colonies.

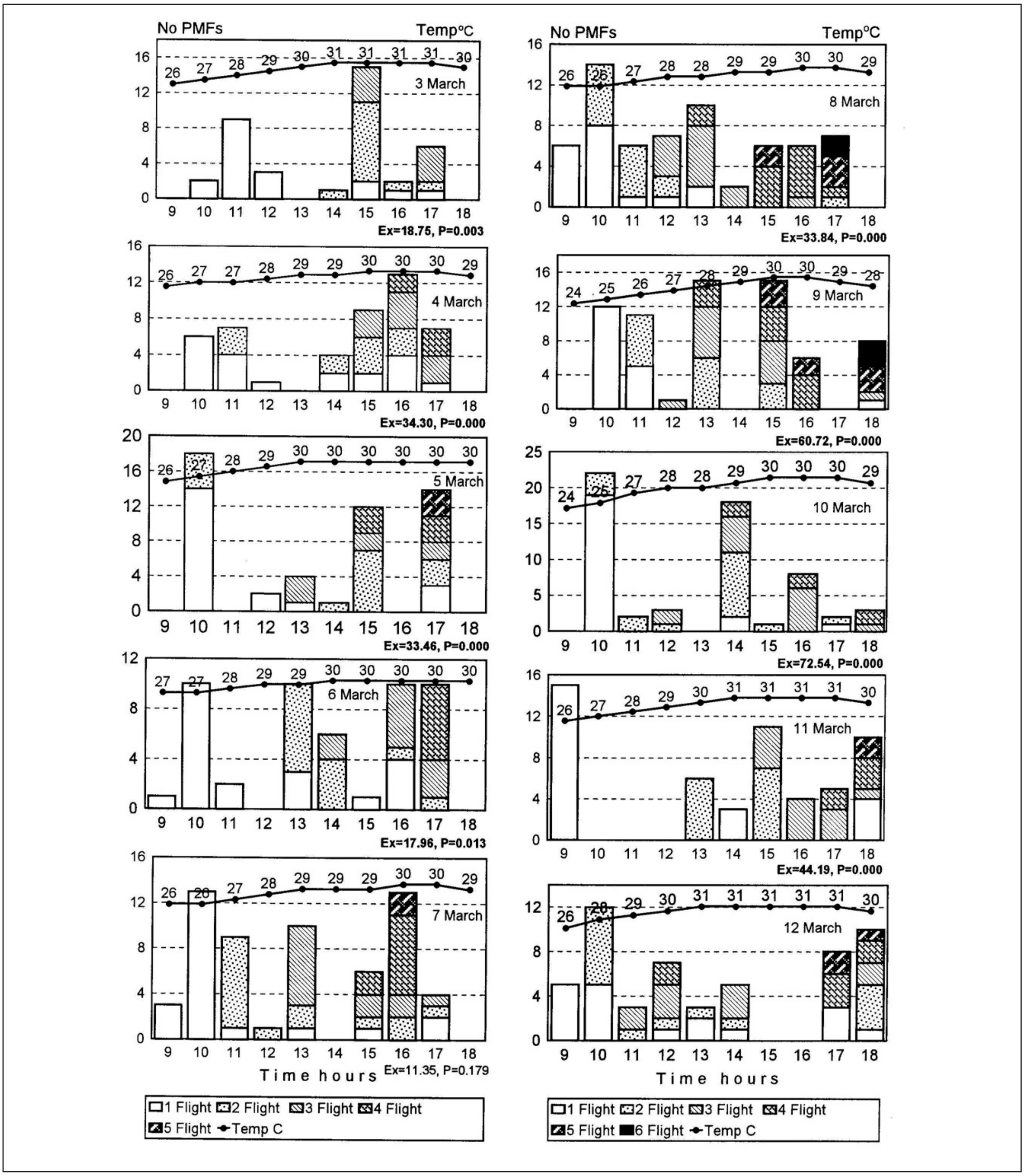

FIG. 2. Frequency distribution (FD) of periodic mass flights (PMFs) at polytechnic site. *Ex* indicates result of exact test and *P* the probability in comparison of FD of the number of PMFs between two successive days. (Bold ***P*** < 0.05 = FD significant).

The quantity of food available at each nesting site was appraised by determining the foraging activities of two colonies of similar size, one from each of the two sites. Figure 1 shows that foraging activity at the polytechnic site at a given time was about 10-times greater than at the banyan tree site. While foragers at the polytechnic were still active at 18:00 h, foraging at the banyan tree was finished by 16:00 h.

Characteristics of colony populations

At the beginning of observations (3 March 2002) there were 19 colonies on the roof of the balcony of the polytechnic building and one each on two trees nearby. Seven swarms arrived in our presence during observations, increasing the total to 26 colonies (table 1).

The banyan tree site had 98 active colonies, 45 empty combs and 16 remnants of fallen combs. Eight of 21 empty combs had between one and nine queen cells. Evidently some colonies had swarmed and others migrated. We observed 82 colonies, six of which migrated in our presence. Five more migrated within two days after the end of observations (13 March). Evidently, the polytechnic site was a place where new swarms were arriving, whereas at the banyan tree site a dearth was in effect and colonies migrating.

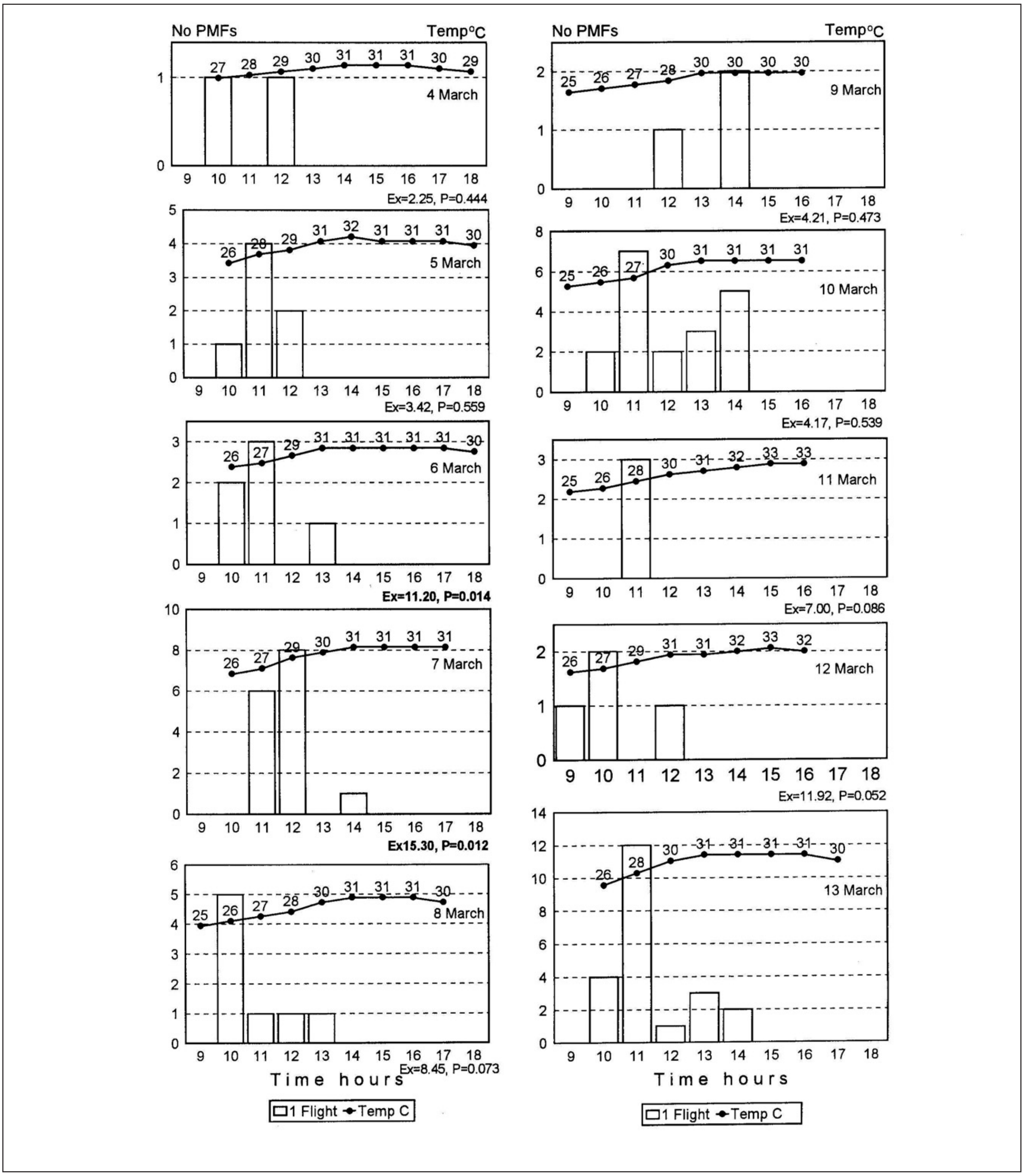

FIG. 3. Frequency distribution of periodic mass flights on banyan tree. For explanations see figure 2.

Percentage of colonies performing periodic mass flights on successive days

Most of the 21–26 colonies (75–91%, 84.3 ± 6.3%, mean ± s.d., n = 10) at the polytechnic site performed at least one PMF (table 1); 59.5% of the colonies performed two PMFs, and 45.4% more than two PMFs per day during the 10 days of observation. The frequency distributions of percentages (transformed to arcsine) of colonies performing first, second, third and fourth PMFs per day during the 10-day period were distributed equally on successive days (first PMF: χ^2 = 1.73, df = 9, P = 0.99; second: χ^2 = 0.79, df = 9, P = 0.99; third: χ^2 = 3.19, df = 9, P = 0.96, and fourth: χ^2 = 4.29, df = 8, P = 0.83, respectively).

On the banyan tree, of the 58–82 colonies only 3.4 to 26.3% (mean 11.3% ± 8.1%, n = 10) performed PMFs on successive days (table 2). None of the colonies performed more than one PMF per day. The percentage frequency of colonies performing PMFs on successive days (transformed to arcsine; 10.6–30.9%, mean 18.5%) did not differ significantly from equal distribution (χ^2 = 14.07, df = 9, P = 0.12).

Number of periodic mass flights performed on successive days

The number of PMFs performed at the polytechnic site by all colonies varied on successive days from 38 to 68 (54.2 ± 6.3, mean ± s.d., n = 10) per day (table 1). However, those numbers

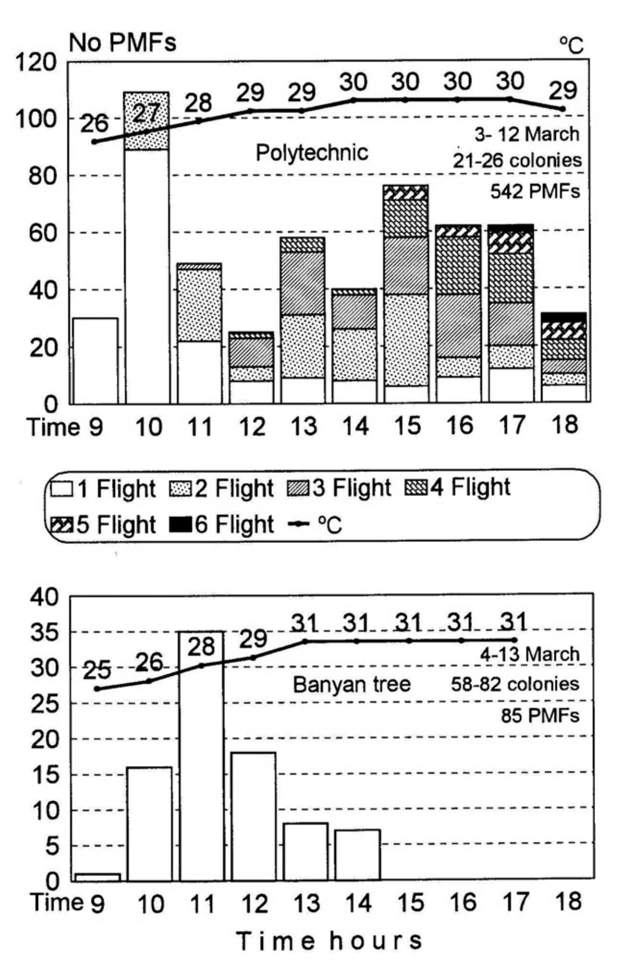

FIG. 4. Pooled frequency distribution of all periodic mass flights performed during 10 days at the polytechnic site and banyan tree.

were distributed equally on successive days (χ^2 = 4.55, df = 9, *P* = 0.87).

The average number of PMFs (8.5 ± 6.8) performed daily by all colonies on the banyan tree was low (table 2). The χ^2 test showed that the frequency of number of PMFs on successive days differed significantly from equal distribution (Ex = 18.94, df = 9, *P* = 0.02) (because the number of colonies changed on successive days, it had to be fitted for the statistical frequency distribution test to the average number of 74 colonies, mean PMFs: 8.4 ± 6.2). However, a large number of 20 PMFs (fitted *n* = 19) was recorded on the last day of observation (13 March). If data recorded on the last day were omitted, then the frequency of the number of PMFs performed on nine successive days was found to be distributed equally (Ex = 12.62, df = 8, *P* = 0.12).

Frequency of PMFs performed daily within one-hour intervals

The colonies at the polytechnic site performed a different number of PMFs during the day (fig. 2). First PMFs were made not only in the morning, but also in the evening. Second and third PMFs were performed between 10:00 and 12:00 h. Thus, it was not the case that first PMFs were performed in the morning and subsequent ones in the evening. Some depression in the number of PMFs was observed around the midday hours.

The frequency distribution of the number of PMFs performed within 1-h intervals differed significantly most commonly between successive days (see *Ex* and *P* > 0.05, fig.2). Only the distributions on 7 and 8 March were similar (*P* = 0.179).

On the banyan tree, the colonies performed not more than one PMF per day. The frequency distribution over the day was mostly similar on successive days (see *Ex* and *P* < 0.05, fig. 3). Only distributions between 6 and 7 March and between 7 and 8 March differed significantly (*P* < 0.05). All PMFs performed during all 10 days at the polytechnic site and on the banyan tree were pooled together according to their respective 1-h intervals (fig. 4). The PMF activity at the polytechnic site lasted 10 h. The 21–26 colonies performed a total of 542 PMFs. They performed 25–109 PMFs within a 1-h interval with an average of 54 flights per hour. At the banyan tree, PMF activity lasted only 6 h, and the 58–82 colonies performed only 85 PMFs. They performed 1–35 PMFs within a 1-h interval with an average of 14 flights per hour.

Thus, the total number of PMFs performed at the polytechnic site was 6.3-times higher, although the number of colonies was three-times higher at the banyan tree. The hourly frequency distribution of the number of PMFs showed two peaks at the polytechnic site and only one at the banyan tree. Before 14:00 h, 50.0% of PMFs were performed at the polytechnic site, and almost all (91.8%) at the banyan tree. The frequency distribution at both sites differed highly significantly (χ^2 = 121.66, df = 9, *P* < 0.0001).

Percentage of individual colonies performing PMFs during different number of days

Not all colonies performed PMFs during all days (table 3). Of 21 colonies present at the polytechnic site during all 10 days, 57% (12) performed PMFs on all days, 14% on eight days, 10% on seven as well as on six days, and only 5% (1) on three as well as two days, respectively. However, at the banyan tree none of the

TABLE 2. Characteristics of periodic mass flights (PMFs) performed by *Apis dorsata* worker bees on the banyan tree.

Date	March 4	5	6	7	8	9	10	11	12	13	Mean	*P** χ^2 *Ex*
Temp. avg °C	29.6	29.9	29.7	29.5	28.9	28.4	28.9	29.8	30.1	29.7	29.5	
No. colonies	58	58	58	82	82	82	82	81	81	76	74	
% colonies making PMFs	3.4	12.1	10.3	17.0	9.8	3.6	23.2	3.7	3.7	26.3	11.3	0.12
No. PMFs	2	7	6	14	8	3	19	3	3	20	8.5	<u>0.02</u>
												0.12
No. PMFs/col.	0.03	0.12	0.10	0.17	0.10	0.04	0.23	0.04	0.04	0.26	0.11	
PMFs/col. making flights	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	

*P = probability of the χ^2 test for equal frequency distribution of the % of PMFs, or exact (*Ex*) test for distribution of the no. PMFs in 10 successive days.
<u>Underlined</u> = for statistical test of equal frequency the no. of PMFs in successive days was fitted to the same mean no. of 74 colonies.
Bold = *P* of *Ex* when the last day (13 March) was omitted.

TABLE 3. Number of PMFs performed by individual colonies during successive days at the polytechnic site.

Colony No.	March										Mean
	3	4	5	6	7	8	9	10	11	12	
1	1	1	1	1	2	1	0	1	1	0	0.9
2	2	1	1	1	1	1	1	0	1	0	0.9
3	1	1	2	1	1	0	1	1	1	0	0.9
4	2	1	2	1	1	0	0	2	1	0	1.0
5	3	4	4	4	4	4	**5**	**3**	3	4	3.8
6	3	4	5	4	4	4	**6**	**2**	3	4	3.9
7	3	3	3	3	4	4	**5**	**2**	3	4	3.4
8	3	4	5	4	4	4	5	4	**3**	**5**	4.1
9	2	3	2	2	2	2	3	4	3	2	2.5
10	0	0	0	1	1	0	1	1	1	1	0.6
11	0	1	0	1	1	1	2	**3**	**1**	0	1.0
12	2	2	3	2	3	**4**	**2**	**4**	**1**	2	2.5
13	1	3	4	4	3	**4**	**2**	**4**	**1**	2	2.8
14	1	0	0	0	0	0	0	0	1	0	0.2
15	3	**4**	**2**	**4**	5	5	**5**	**3**	4	4	3.9
16	3	**4**	**2**	**4**	5	5	**6**	**3**	5	4	4.1
17	3	3	2	3	4	**6**	**4**	4	5	4	3.8
18	3	3	2	3	4	6	**5**	**3**	4	3	3.6
19	2	2	2	2	3	5	4	**4**	**2**	2	2.8
20	0	1	1	0	0	0	0	1	0	0	0.3
21	1	1	1	1	0	0	0	1	0	1	0.6
22		**1**	**5**	**2**	**4**	**3**	**5**	**3**	**3**	**5**	3.4
23			1	1	1	1	0	0	0	0	0.5
24					**2**	**4**	4	4	**3**	**1**	3.0
25								3	**4**	**2**	3.0
26										3	3.0
Total PMFs	38	47	50	49	59	64	68	60	54	53	542

Bold numbers indicate high number of PMFs per day followed by day with low number of flights, or contrary (difference 2 or 3 PMFs).
Underlined indicates successive groups in which a total of identical or similar numbers of PMFs per day were performed.

colonies performed PMFs during all days. Only 1% (1), 4%, 23% and 40% (33) of colonies performed PMFs during five, three, two, and one days, respectively, whereas 32% (26) colonies at the banyan tree site did not perform any PMF on all 10 days. Thus, a much higher percentage of colonies at the polytechnic site performed PMFs during more days (2–10) than at the banyan tree site (0–5).

Number of PMFs performed by individual colonies on successive days

Individual colonies at the polytechnic site performed 0–6 PMFs per day on 10 successive days (table 3). Because not all colonies performed PMFs during all days, the average number of PMFs per day fell below one in some colonies. At the polytechnic site, the mean numbers of PMFs performed per day by individual colonies ranged from 0.2 to 4.1 (table 3). The overall mean of PMFs per day was 2.23. Congregation of all data was skewed (skewness = – 0.26), and therefore the median was 2.8. The density trace revealed that distribution of the mean number of PMFs per day showed two frequency peaks, one at 0.7 and the other at 3.4 PMFs per day.

In contrast, at the banyan tree none of the 82 colonies performed more than one PMF per day during the 10 days of observation.

It is intriguing that the same colonies did not perform a similar number of PMFs under similar conditions on successive days. Fluctuation in the number of PMFs was observed (table 3). An increase or decrease in number by one flight was noticed during several successive days. It is interesting to note that the highest number of PMFs often followed the performance of the lowest number on the previous day; the reverse was also true (bold in table 3). As a result, within PMFs performed by 26 colonies during 10 days, 59 successive cycles of two or three days were observed in which the total number of PMFs was identical or similar (underlined in table 3).

Intensity of PMF activity

Intensity of successive PMFs was examined in detail in 13 individual colonies which performed at least four flights a day during the seven days in which intensity was recorded (6–12 March, $13 \times 7 = 91$ colony flight days). Each grade intensity (1–5) presented a determined number of bees (6–44, see methods) flying in a selected area (50×40 cm) near the nests. High

TABLE 4. Intensity of PMFs performed at the polytechnic site by individual colonies which made several flights per day. First row-intensity in 5-grade scale (1st grade = 6 bees, 2nd = 12, 3rd = 23, 4th = 33, 5th = 44). Second row-total number of worker bees participating in all daily flights visible in a pre-determined area of 50 × 40 cm near the nests. Third row-means instead of extreme values in 2-day cycles (in parentheses).

Colony No.	March 6	7	8	9	10	11	12	Mean	*P* for χ^2#
5	**5,3**,3,2	**2,5**,3,3	3,3,**1,5**	3,3,3,4,3	5,5,4	5,5,4	5,**5,3**,3		
	103	103	96	124	122	122	134	114.9	**0.514**
6	4,**5,3**,3	**3,5,2,4**	3,4,4,3	4,**4,1**,3,3,3	4,4	4,5,4	**3,5,4,2**		
	123	113	111	141	66	110	113	111.0	0.016
	(118	118)*	(126	126)	(88	88)	113	111.0	**0.264**
7	**3,1,3**	2,**1,3**,2	**1,3,1,3**	2,**2,4**,3,2	3,2	3,4,3	3,4,3,3		
	52	56	58	96	36	79	101	68.3	0.000
	52	56	58	(66	66)	79	–	62.8	**0.607***
8	**5,2,4,1**	**4,2**,3,4	3,**3,5**,4	**5,3**,3,**3,5**	4,**5,3**,3	4,**5,3**	**3,5,3**,3,2		
	97	102	123	157	123	100	126	118.3	0.096
9	**2,5**	**1,4**	**1,5**	2,3,4	3,3,2,3	3,**3,5**	4,3		
	68	39	51	69	82	90	56	65.0	0.020
	(54	54)	51	69	82	(73	73)	65.0	**0.346**
12	5,5	**3,5,3**	5,**5,1,5**	4,5	**4,2,4**,3	5	**1,3**		
	89	90	140	77	102	44	29	81.6	
	89	90	(109	109)	(73	73)	-	90.5	**0.205***
13	3,3,**1,4**	**2,4**,4	1,**2,5**	3,4,3	**3,5,3**,3	4	2,2		
	85	79	64	79	113	33	27	68.6	0.000
	85	79	64	79	(73	73)	-	75.5	**0.881***
15	**5,2,4**,3	2,**1,4**,3,2	2,2,**3,5,3**	**2,5**,4,**2,5**,4	5,5,4	4,5,4,4	**3,5,3**,2		
	113	89	117	191	122	143	103	125.4	0.001
	113	(132	132	132)	122	143	103	125.4	**0.604**
16	3,4,5,4	3,2,**2,4**,3	3,3,4,4,3	4,**1,5**,3,4,3	5,5,4	5,**5,1**,4,4	5,4,4,4	137.1	
	133	105	134	162	122	161	143	137.1	**0.155**
17	**5,3**,2	**2,4**,3,3	**2,5,2,2,4**,3	**3,5**,4,4	4,3,4,4	4,5,**4,2**,3	4,3,4,3		
	81	92	140	133	122	146	111	117.9	0.013
	81	(116	116)	133	122	(129	129)	117.9	**0.182**
18	4,**4,1**	**1,5,2,4**	**1,3,1,2,4,2**	**5,3**,4,**4,2**	4,4,3	4,**4,1**,3	4,3,4		
	72	97	95	146	89	95	89	97.6	0.026
	72	97	95	(118	118)	95	89	97.6	**0.223**
19	**4,2**	3,**4,2**	2,3,3,3,3	**5,2**,4,4	4,3,3,3	4,3	4,3		
	46	69	105	124	101	56	56	79.6	0.000
22	4,4	**3,1,1,4**	3,2,2,	3,**2,5,2**,4	4,3,4	4,**4,1**	**1,5,4,2**,2		
	66	69	49	127	89	72	110	83.1	0.000
	66	69	(88	88)	89	(91	91)	83.1	**0.114**

Bold numbers of PMF intensity indicate the highest intensity per day followed by the lowest, or contrary.
Underlined indicates the highest total no. of flying bees followed by the lowest, or contrary. In (parenthesis)-means of the underlined data. #-probability of the χ^2 test for equal frequency distribution
bold P indicates equal distribution.
* the last day was omitted in frequency calculation because it probably belonged to an absent 2 day cycle.

variation from grade 1 up to 5 was noticed in PMFs performed by particular colonies within one day (table 4). Variation of one grade more or one less was noticed in several successive flights. However, we observed also that PMF flight of the lowest intensity (grade 1) was followed by flight of the highest intensity (grade 5) and vice versa. Altogether, 91 times PMFs of lower intensity were followed by flights of higher intensity (difference of at least 2 grades between 2 successive flights) or vice versa (table 4). The cycles of two opposite flight intensities were observed in 61.5% (56) of the 91 colony flight days performed by all 13 colonies during seven days.

Since each grade intensity of PMF (1–5) represented a determined number of bees (6–44), the total number of bees (TNB) participating in all PMFs (1–6 in that area) performed on a particular day could be calculated (table 4). The TNB in individual colonies varied on successive days. More or less similar TNB were recorded on some successive days. However, a day with low TNB was followed by a day with high TNB and vice versa (high followed by low). The 2-day cycles (underlined in table 4) occurred in 69% (9) of the 13 examined colonies.

The frequency of TNB on successive days was distributed equally only in two colonies (5 and 16). However, when the 2-day cycle was treated as unity, then the extreme values of TNB were replaced by their means (in parenthesis in table 4). After those two-day cycles were applied, the $P < 0.05$ values for the χ^2 test showed equal distribution of the frequency of TNB in successive days (*P* bold in table 4) in almost all colonies.

In colony numbers 7, 12 and 13, the TNB on the last day had to be omitted from statistical calculations because they belonged to a 2-day cycle, of which the second day occurred after termination of the observation. In colony no. 15 a 3-day cycle had to be applied.

The correlation between the number of PMFs per day (table 3) and total number of bees participating in those flights (TNB, table 4) on successive days was found significant only in three colonies (6, 8 and 22, $r = 0.91$, $P = 0.00$; $r = 78$, $P = 0.04$; and $r = 0.78$, $P = 0.04$, respectively). In the rest of 76.9% (10) of colonies, such correlation was not significant. This indicates that the higher number of PMFs per day was compensated by lower intensity flight.

Number and intensity of PMFs performed by individual colonies in relation to comb size and brood amount

Depending upon the amount, type and arrangement of brood, the colonies at the polytechnic building were divided into four groups reflecting the time they stayed at the site (table 5).

Colonies in groups which stayed at the polytechnic building a longer time had on average significantly larger combs (table 5). However, this was not true for individual colonies. Comb size of colonies within the same group varied. Comb size of colonies that arrived later (group 2) was similar or even larger than in colonies which stayed longer.

Honey was not visible in combs of colonies in group 1. However, in colonies of groups 2, 3 and 4 honey occupied a 3-, 4- and 5-cm wide upper part of the combs, respectively. Brood occupied the rest of the combs in quantities of 4.7, 22.0, 24.3 and 31.4 dm^2 in the four respective groups. Unsealed brood occupied the total brood area of 4.7 dm^2 in group 1. Semicircles of sealed and unsealed brood were present in the other groups. In group 2, the upper three-quarters of the length of the radius covered sealed brood which represents 9/16 of the brood area. Thus, unsealed brood occupied 7/16 of the area (43.8% or 9.6 dm^2). In group 3, the upper half of the radius covered unsealed brood which represented a quarter of the brood area or 6.1 dm^2. In group 4, unsealed brood occupied a 5–7 (mean 6) cm wide area between the upper and lower sealed brood area as well as 5-cm wide marginal area. The radius sections of 25, 6, 23 and 5 cm covered sealed and unsealed brood area alternatively. Calculations revealed that unsealed brood occupied 25.9% of the area (9.0 dm^2). Thus, unsealed brood occupied 4.7, 9.6, 6.1 and 9.0 dm^2 in the four groups, respectively.

Individual colonies performed statistically different average number of PMFs per day (table 5). However, similar mean numbers of flights per day were observed in different groups. Surprisingly, although the mean size of combs in group 4 was seven-times higher than in group 1, the difference between mean numbers of PMFs per day in four groups of differently developed colonies was not found significant. Similarly, correlation between comb size and mean number of PMFs performed per day was not found to be significant either for individual colonies or for group means (table 5).

The relationship between size of combs and intensity of PMFs (total number of bees, TNB) performed by colonies at the polytechnic site was also examined (table 5). TNB participating daily in PMFs of individual colonies differed significantly. Interestingly, TNB in some smaller colonies was higher than in larger colonies. Despite the fact that mean sizes of combs were in some groups several times higher than others, the means of TNB in the four groups of colonies did not differ significantly (table 5). Similarly, the correlation between size of the combs and intensity of PMFs was not significant either for individual colonies or for the four groups of colonies.

Because we had no direct access to the nests on the banyan tree, detailed determinations were not made of the type and amount of brood nor the size of occupied combs. However, in nests which were covered with a thin layer of bees (because part of the bees had swarmed), a 2–7 cm-wide belt of sealed brood could be detected. Similar amount of brood could be observed in some colonies while they performed PMFs. Combs of colonies which migrated in our presence had single sealed brood cells on the surface of combs and congregations of additional cells along the side and bottom edges of the combs. This indicated that those colonies had ceased rearing young brood for almost tree weeks.

The size of eight combs fallen on the ground varied from 72 × 60 cm to 144 × 96 cm with a mean of 106 × 81 cm. The area of comb ranged from 33 to 108 dm^2 with a mean of 69.4 ± 24.9 dm^2. We assume that the combs of the nests on the tree were of similar size. Thus, the combs on the banyan tree were twice as large as combs of group 4 colonies (34.45 dm^2) which stayed at the polytechnic site for the longest time. Despite the large combs on the banyan tree, the bees at the polytechnic site performed daily about 20-times more PMFs per colony (2.3) than those on the banyan tree (0.11).

DISCUSSION

We found that *A. dorsata* colonies under similar environmental conditions performed similar PMF activities over 10 successive days. This was the key question raised in the introduction. Moreover, the PMF activities of one population differed significantly from those of another under different environmental conditions. Seven and half times more colonies performed PMFs at the polytechnic site (84.3%) compared to the banyan tree site (11.3%). The daily average number of PMFs per colony at the polytechnic site (2.3) was about 20-times higher than at the banyan tree (0.11). The distribution of the number of PMFs over the day was also different at both sites.

The environmental conditions at both sites were different. Rich food resources were available at the polytechnic site, while a dearth prevailed at the banyan tree site. The polytechnic site was characterized by an active period of arrival and colonization of new swarms. Growth and development were obvious at this site, whereas at the banyan tree the colonies were ceasing brood production and preparing to migrate. We suggest that the differences in PMF activities between the two sites were due to different environmental conditions.

It is of ecological significance to know why colonies perform PMFs differently even under similar meteorological conditions, like at the polytechnic and banyan tree sites. One of the suspected functions of PMFs is to facilitate defecating by young worker bees. A comb with more unsealed brood stimulates young workers to feed larvae and consume pollen. Consequently, the worker bees produce more faeces and are more

TABLE 5. Status of *Apis dorsata* colonies at the polytechnic site on 10 March 2002 and mean

	Group 1. No sealed brood, colonies stayed at place up to 8 days #			Group 2. Sealed brood in upper part of combs, from 8 to 21 days	
Colony number	22	24	25	15	18
Comb size, length × height cm and surface dm^2	35 × 25	30 × 20	15 × 10	90 × 30	70 × 50
	6.9	4.7	2.4	21.2	27.5
Group mean of the surface dm^2	4.66a				24.35b
Mean number of PMFs per day	3.4abc	3.0abc	3.0abc	4.0bc	3.6abc
Group mean of the number of PMFs	3.1a			3.8a	
Intensity expressed in total number of bees participating daily in all PMFs, visible in determined area of 50 × 40 cm	83.1abc	85.4abc	75.7abc	125.4ef	97.6bcde
Group mean of PMF intensity	81.4a			111.5a	

Probable number of days the colonies stayed at the place after arrival; different letters after means indicate significant differences $P < 0.05$.
*r, P indicates correlation and probability between comb size and both number and intensity of PMFs.

likely to perform PMFs. Thus, we suggest that the number and intensity of PMFs performed by a particular colony depends in part upon the amount of unsealed brood.

Our results showed that 10-times more foragers collected food at the polytechnic site compared to the banyan tree. Nagaraja & Rajagopal (2000) reported a correlation between the number of foragers returning to the nests and the amount of brood in the comb. Thus, the amount of brood in the nests at the polytechnic site was probably also several times higher than at the banyan tree. This is confirmed by our observations of some colonies which uncovered brood while performing PMFs. Sealed brood was limited to a belt along comb edges. It is generally known that *A. dorsata* colonies stop rearing larvae well before migration. The colonies usually migrate when all or most workers emerge from the combs. Thus, for at least two weeks before migration only sealed brood is present in the combs. Hence, more open brood was likely present at the polytechnic site than at the banyan tree. This explains the significantly higher PMF activities performed at the polytechnic site.

There are considerable differences between our results and those reported by Woyke *et al.* (2004). In the present study we did not find significant differences in PMF activities within *A. dorsata* populations over 10 successive days. However, Woyke *et al.* (2004) reported significant differences in PMF activities recorded over a three-month period. While environmental conditions and status of colonies were similar during the 10 successive days of our present observations, they were more variable during the longer three month period of the earlier study. This supports the conclusion that PMF activities are related to environmental conditions and, by extension, the energetic/nutrient status of the colonies.

Some colonies do not perform PMFs for several days. Surprisingly, worker bees from as many as 32% of the colonies on the banyan tree did not perform any PMF for 10 successive days. Worker bees that did not perform PMFs also could not defecate. This phenomenon of non-performance of PMFs and non-defecation is rare and intriguing. However, Woyke *et al.* (2005) showed that worker bees from all colonies perform mass flights and void faeces every day at the time of the so-called dusk drone flights. If workers from some colonies accumulated little faeces and voided them at the dusk mass flights, there is no need to perform PMFs to defecate at daytime.

Interesting is the finding that individual colonies perform different a number of PMFs on successive days. We suggest a possible explanation. When many or most of the young workers void faeces while performing four, five or even six PMFs in a day, there is no need to perform so many flights the next day. Therefore, the next day only one, two or even three PMFs are performed. However, after several days when only two or three PMFs per day are performed, relatively larger numbers of workers with accumulated faeces appear. Consequently, a greater number of four to six PMFs per day is performed on the following day. Our results showed that similar or identical numbers of PMFs were performed not in successive days, but within successive cycles of two or three days.

Similarly, the intensity of successive PMFs performed per day varied. PMF of low intensity was followed by flight of high intensity or vice versa. The explanation is similar as above. When relatively few workers participated in a PMF more workers with faeces accumulated in the nest, and therefore more of them participated in the following flight, or vice versa.

Our results also showed the presence of two-day cycles in the total number of workers participating in all PMFs performed on successive days. The explanation is as above.

Surprisingly, no correlation was found between the size of combs the colonies occupied and the number and intensity of PMFs. This is unexpected. However, larger combs need not necessarily have more unsealed brood. In our investigation, the small combs of group 1 at the polytechnic site were full of unsealed brood. The larger combs of groups 2–4 which stayed at the site up to 40 days were full of sealed brood. However, unsealed brood occupied only half of the brood area in group 2 and only one-fourth that area in groups 3 and 4. Thus, unsealed brood occupied 4.7, 9.6, 6.1, and 9.0 dm^2 in the four respective groups.

The proportions are understandable. When only unsealed brood is present it occupies 100% of the brood area. When all stages of brood development are present and the queen is not restricted in egg laying, then unsealed brood should occupy about one-third of the area because development times of unsealed brood

number of PMFs and their intensity per day for four groups of differently developed colonies.

Group 3. Sealed brood in lower part of combs, colonies stayed from 21 to 28 days			Group 4. Two separated areas of sealed brood, upper and marginal, colonies stayed from 29 to 42 days				r, P*
9	16	19	5	6	8	17	
75 × 50 29.4	60 × 45 21.2	80 × 50 31.0	80 × 60 37.7	70 × 60 33.0	80 × 60 37.7	75 × 55 32.4	
	27.20b			35.20c			
2.5a	4.1c	2.8ab	3.8bc	3.9bc	4.1c	3.8bc	0.36; 0.25
3.1a			3.9a				0.65; 0.35
65.0a	137.1f	79.6ab	114.9def	111.0cdef	118.3ef	117.9ef	0.40; 0.19
93.9a			115.5a				0.84; 0.16

present one-third of the total development. When the colonies occupy the nest shorter then 21 days as in group 2, the proportion of unsealed brood should be higher than one-third. However, when colonies occupy nests longer than 21 days and the queen is restricted in egg laying by lack of sufficient empty comb, the proportion of unsealed brood should be lower than one-third of the brood area, as happened in groups 3 and 4.

Thus, although the proportions of extreme values of mean comb sizes were *c.* 1:7.6, the proportions in unsealed brood area were *c.* 1:2 , and in mean number and intensity of PMFs *c.* 1:1.3-1.4. Consequently, the new colonies performed a similar number of PMFs as those which stayed longer. Perhaps workers of new colonies eat more honey and pollen to construct new combs, consequently producing more faeces. It is likely that the amount of unsealed brood is not the only factor determining PMF activity. The number of workers in the new colonies with small combs was probably similar to that in older colonies.

However, the number of bees in colonies was not the main factor determining PMF activity. On the banyan tree the combs were twice as large (69.4 dm^2) as the largest at the polytechnic site (34.5 dm^2). Probably the number of bees was also larger in colonies at the banyan tree. However, little or no open brood was present at the banyan tree because colonies were preparing to migrate and not rearing brood. Consequently, the average daily number of PMFs per colony was 20-times higher at the polytechnic site (2.3) than at the banyan tree (0.11). These findings explain the low insignificant correlation between comb size and PMF activities.

A summary of our present results and those published earlier indicates that measures of PMF activity are similar within *A. dorsata* populations recorded over a short period (10 days). However, variations are significant in PMFs recorded over longer periods (several months). We suggest that this is due to changing environmental conditions and, by extension, changing energetic/nutrient demands of colonies, among which the amount of unsealed brood is an important factor. All results show that PMF activities play an important role in brood rearing.

Acknowledgements

We would like to thank Prof. Dr hab. Halina Woyke for help in the analysis and presentation of the data in this paper.

REFERENCES

ASHTON, P S; MESELSON, M; ROBINSON, J; PERRY P; SEELEY, T D (1983) Origin of yellow rain. *Science* 222: 336–368.

KASTBERGER, G; WINDER, O; HOETZL, T; RASPOTING,G (1996) Behavioural features of a periodic form of massed flight activity in the giant honeybee *Apis dorsata*. *Apidologie* 27: 381–395.

MARDAN, M; KEVAN, P G (1989) Honeybees and yellow rain. *Nature* 341: 191.

MEDDOX, J (1984) Natural history of yellow rain. *Nature* 309: 207.

MEHTA, C; PATEL, N (2002) *StatXact 5, User manual*. Cytel Software Corporation; Cambridge, MA., USA

MUTHURAMAN, M; SRINIVASAN, G (2002) Some observations on the cleansing behaviour of rock bees (*Apis dorsata* Fabr.). *VI Asian Apicultural Association International Conference, Bangalore*. Abstracts: 45.

NAGARAJA, N; RAJAGOPAL, D (2000) Foraging and brood rearing activity of rock bee *Apis dorsata* F. (Hymenoptera : Apidae). *Journal of Entomological Research* 24: 243–248.

REDDY, C C (1983) Studies on the nesting behaviour of *Apis dorsata* F. *Proceedings of the 2nd International Conference on Apiculture in Tropical Climates, New Delhi, India*; pp. 391–397.

REDDY, M S; REDDY, C C (1987) Rates of colonization and de-colonization in rock-bee *Apis dorsata* Fabr. *Indian Bee Journal* 49: 3–4.

SEELEY, T D; NOWICKE, J W; MESELSON, M; GUILEMIN, J; AKRATANAKUL, P (1985) Yellow rain. *Scientific American* 253: 128–137.

SOKAL, R R; ROHLF, F J (2000) *Biometry*. W H Freeman & Co., New York, USA (3rd edition).

VENKATESH, G; REDDY, C C (1989) Influence of swarm size on comb size of the giant honeybee. *Proceedings of Indian Academy of Science. (Animal Science)* 98: 425–430.

WOYKE, J; WILDE, J; WILDE, M (2001) Swarming, migrating, and absconding of *Apis dorsata* colonies. *7th IBRA Conference on Tropical Bees, and 5th Asian Apicultural Association Conference, Chiang Mai*; pp. 183–188.

WOYKE, J; WILDE, J; WILDE, M (2003) Periodic mass flights of *Apis laboriosa* in Nepal. *Apidologie* 34: 121–127.

WOYKE, J; KRUK, C; WILDE, J; WILDE; M (2004) Periodic mass flights of the giant honey bee *Apis dorsata*. *Journal of Apicultural Research* 43: 180–185.

WOYKE, J; WILDE, J; WILDE, M; REDDY, C C; CERVANCIA, C (2005) Worker bees often predominate in dusk 'drone flights' of the giant honey bee *Apis dorsata*. *Journal of Apicultural Research* 44: 129–131.