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Periodic mass flights of the giant honey bee, *Apis dorsata*

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SUMMARY

This article reports observations conducted in Rampur, Chitwan, Nepal, during March–April and October–December 1999. 14 continuous observations were carried out from 08:00 h to 19:00 h on 6 to 48 nests of *Apis dorsata* in different seasonal conditions. Detailed observations of 410 periodic mass flights (PMFs) were recorded. During the day, *A. dorsata* workers made 0– 6 PMFs, each of which lasted about 5 min. Worker bees from 52% to 100% of colonies performed PMFs within a day. About 55% of colonies performed a second PMF and about 25% a third flight. Percentage of colonies performing PMFs and the number of PMF activities per colony were highest when the largest amount of brood was present in colonies. In cool conditions (average temp. 20.9 °C), PMF activity lasted between 4 and 7 h and peaked around noontime. In warm conditions (average 26–28 °C), the duration of this activity extended up to 9 h with no PMFs at noon. In hot conditions (average 33.6 °C), the duration of PMF activities was extended to 11 h; however, flights were made only in the morning between 8:00 h and 10:00 h and in the evening between 16:00 h and 18:00 h, with a 6-h gap of no PMF in between. The duration and distribution of PMF activities during the day were correlated with average daily temperatures. On the warmest days, more PMF activities (63–67%) were performed after the hottest midday hours were over. We suggest that both the short duration of 5 min of PMF activity as well as the distribution of PMFs during the day are strategies to avoid thermal disruption of the protective bee curtain.

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

INTRODUCTION

Apis dorsata workers forming the nest curtain make short periodic mass flights (PMFs). Such flights are linked with defecation, which was misinterpreted as 'yellow rain' (Ashton *et al.*, 1983; Meddox, 1984; Seeley *et al.*, 1985). Mardan & Kevan (1989) and Mardan & Ashaari (1990) referred to this phenomenon as 'en masse flight' and suggested that defecation assists in nest temperature regulation. Detailed observations of phenomena occurring during one mass flight in and around a colony were described by Kastberger *et al.* (1996). According to Muthuraman & Srinivasan (2002), the comb became partially exposed during such flights. Different behavioural phenomena of colonies observed in this investigation (except PMFs) were described by Woyke *et al.* (2001).

PMFs are performed daily and must play an important role in the life of the colonies. However, the role and characteristics of PMFs are not fully understood. The purpose of this investigation was to determine which phenomena influence variation in PMFs. These results could help explain this behaviour as well as geographic, climatic and seasonal variations in its expression.

MATERIALS AND METHODS

Observation procedures

The investigations were conducted at the campus of the Institute of Agriculture and Animal Science of the Tribhuven University in Rampur, Chitwan, Nepal, (latitude 27°39' North, longitude 84°21' East, altitude 190 m above sea level) from 5 March to 2 April and from 18 October to 20 December 1999. Six to 48 nests of *A. dorsata* were observed from 8:00 h to 19:00 h (local time = + 5.45 h GMT) during 14 whole-day examinations. Together, 410 PMFs were observed. In the spring, observations were made on 25 colonies over three days under different meteorological conditions. Of those colonies, 19 were located on one building (one migrated in March) and six on another. Two colonies on the first building were weak (nest area 0.5 x 0.3 m), while all others were strong with nest sizes about 1.5 x 0.7–1.0 m. Altogether, 118 PMFs were recorded within the three whole-day observations on both buildings (96 and 22 flights on each, respectively). In autumn, colonies were observed at weekly intervals on the tower of a water tank. At the beginning of observations, nine colonies were found there. That number increased to 48 by 14 December (fig. 1). Because it was difficult to record the large number of PMFs performed by these colonies, the last observations (20 December) were made on 17 colonies on the first building observed in March. Altogether 292 PMFs were observed in autumn.

The nests on the two buildings were observed from a distance of 4–5 m, and on the water tank tower from a distance of 12 m. Observations were made with the aid of 12 x 50 binoculars. One colony was observed at least once per week through a window from a distance of 0.5 m. The activities of the workers were recorded with a video camera recorder provided with a x 24

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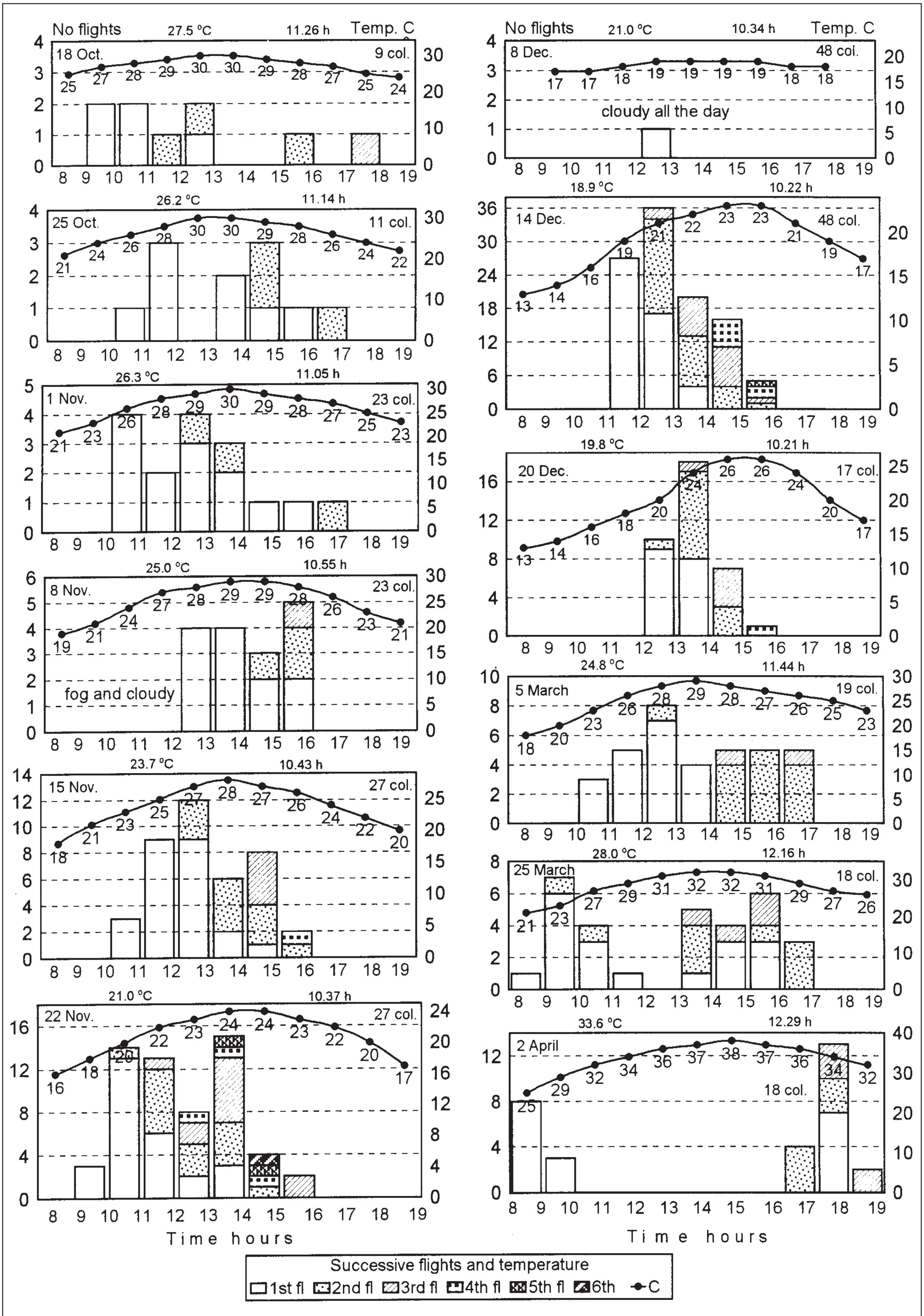

FIG. 1. Frequency distribution of periodic mass flights performed by *Apis dorsata* worker bees. The temperature above the upper frame line indicates average daily temperature, the time over that line indicates the duration of the day. col. - number of colonies.

TABLE 1. Characteristics of periodic mass flights (PMFs) of *Apis dorsata* workers performed in autumn.

Meteorological conditions	Warm period (1)				Cool period (2)			
Date	18 Oct	25 Oct	1 Nov	8 Nov	15 Nov	22 Nov	14 Dec	20 Dec
Temp. avg °C	27.5	26.2	26.3	25.0	23.6	21.2	18.9	19.8
No. colonies observed	9	11	23	23	27	29	48	17
No. PMFs observed	9	11	16	16	40	60	104	35
Avg PMFs per colony	1.0	1.0	0.7	0.7	1.5	2.1	2.2	2.1
% colonies making PMFs	56	73	70	(52)	89	100	100	100
Duration PMF activity h	9	7	7	(4)	6	7	5	4
Duration midday gap h	2	1	–	–	–	–	–	–
( ) 8 November, day partly cloudy, see fig. 1.								
Percentage of colonies performing different number of flights								
2 PMFs at least	33	27	13	13	41	55	67	76
3 PMFs at least	11	0	0	4	15	38	35	24
4 PMFs at least	0	0	0	0	4	10	15	6
5 PMFs at least	0	0	0	0	0	7	2	0
6 PMFs	0	0	0	0	0	3	0	0

optical zoom. Air temperature and relative humidity were recorded every hour with an electronic thermo hygrometer placed in the shade, 1.5 m above the ground, 5 m away from the buildings or the tower.

The size of combs and amount of brood were checked every seventh to tenth day on the two buildings and on another smaller accessible water tank tower. For that purpose, the curtain bees were smoked out to uncover the comb.

Because *A. dorsata* swarms started to arrive in October and migrated in April, the results are presented according to the biological rhythm of the colonies; with the autumn ones first and then the spring.

Some *A. dorsata* PMFs are presented in the online version.

Statistical analysis

Arcsine transformation was applied to proportions. ANOVA was used to compare variances. Significant differences between particular means were detected by LSD analysis. The *t* test was applied to determine significant differences between two means. Some data within the frequency distribution of the number of PMFs performed within hourly intervals were lower than five. Therefore, exact *P*-values (Ex) were computed using R x 2 contingency tables (Mehta & Patel, 2002) to compare distribution of PMFs performed by worker bees in different days or by different populations in the same day. Goodness-of-fit χ^2 test was used to compare distribution of PMFs and expected frequencies (Sokal & Rohlf, 2000). Calculations concerning time were made in minutes. The results are presented in hours and minutes. Statistical tests were made with Statgraphics or StatXact softwares.

RESULTS

Seasonal meteorological conditions

Different meteorological conditions prevailed during the seasonal observation periods. In the autumn from 18 October to 8 November the overall average temperature was 26.2 °C. We call this period 1 and designated it as 'warm' (table 1). In period 2 from 15 November to 20 December the overall average was 20.9 °C. We designated this period 'cool'. In the spring (table 2), 5 March (average temp. 24.8 °C) was designated 'cool', 25 March (28.0 °C) as 'warm', and 2 April (33.6 °C) as 'hot. The overall mean spring temperature was 28.8 °C. The LSD test (95.0%) showed that the overall mean temperature during the cool autumn period was significantly lower than that at both the warm autumn and the overall mean spring temperature. However, no significant difference was found between overall means at the warm autumn period and the spring.

Status of *Apis dorsata* colonies

Swarms started arriving at the beginning of October. Colonies had the largest amount of brood in December and started to swarm and migrate at the end of March. Table 1 shows that on 18 October in the beginning of observations, nine colonies were found on the tower of the water tank. Five of them were broad and very flat, adhering to the top substrate. Apparently, they had very small combs or perhaps some no combs. Over the next few weeks, more swarms arrived. However, in the meantime some migrated. They left behind small white combs (15 x 20 cm). No brood was reared in these combs. As time passed more swarms arrived and the nests became deeper and slimmer. The workers constructed combs inside and reared brood. Progressively, the size of combs increased, as well as the amount of brood. Colonies were in maximal development in December (nest sizes 1.5 x 0.7–1.0 m), and combs were full of brood. In February the colonies started to swarm. Queen cells were found at the lower edge of the combs. At this time the brood was not present in the whole comb. Only a band of brood 10–15 cm wide was observed along the edges of the combs. Thus, although the colonies were large, there was less brood than in December. In April, after the brood emerged, the last swarms migrated leaving empty combs in about half of the original colonies. In the rest of the colonies, enough workers remained to cover the combs. The queens started to lay eggs and the amount of brood increased progressively.

Periodic mass flights

Young naïve workers comprise a large proportion of the bees in the nest curtain. Undisturbed *A. dorsata* workers made PMFs during the day. Over a short period, complete disorder of the curtain occurred. In some colonies, we observed the disorder 2–3 min before the start of the PMFs. The workers flew out en masse, giving the appearance of a swarm. The workers flew in

TABLE 2. Characteristics of periodic mass flights (PMFs) of *Apis dorsata* workers performed in spring.

Meteorological conditions	Cool day (3)	Warm day (4)	Hot day (5)
Date	5 March	25 March	2 April
Temp. avg °C	24.8	28.0	33.6
No. colonies observed	19	18	18
No. PMFs observed	35	31	30
Avg PMFs per colony	1.8	1.7	1.7
% colonies making PMFs	100	100	100
Duration PMF activity h	7	9	11
Duration midday gap h	–	1	6
Percentage of colonies performing different number of flights			
2 PMFs at least	74	50	39
3 PMFs at least	11	17	28

circles up to about 20 m from nests. PMF activity of a single colony lasted between two and 10 min (average ± s.e.: 4 min 47 sec ± 7 sec (n = 130), mode: 5 min). However, the standard skewness (4 min 58 sec) indicates a slight skewed distribution in the direction of higher values. Workers returning from the flights landed everywhere on the curtain surface. The characteristic defensive circular wave, which occurs when a worker lands on the curtain outside the mouth zone, was not observed during PMF activity while the curtain was in disorder.

Only sporadically would a drop of faeces fall on us, even while we stood under a tower with 65 nests while 48 of them were engaged in PMF observations. About 10–20 faecal spots per m^2 could be found on the nearby vegetation.

Percentage of colonies performing periodic mass flights

During the first autumn period (18 October–8 November), up to about 50% of colonies did not make PMF on some days (table 1). On average, only 63% of colonies performed PMFs during the first warm period compared to as many as 97% during the second cool one, a significant difference (t = 5.69, P = 0.001). All colonies performed PMFs in the spring (table 2). Correlation between the percentage of colonies performing PMFs during the whole observation period and daily average air temperature was not found to be significant (r = 0.03, df = 12, P = 0.92).). The 8 December (not presented in table 1) was overcast all day. Only one colony performed PMF under such conditions.

Number of periodic mass flights per colony

On average, 0.85 and 1.98 PMFs per colony were performed during the first and second autumn periods, respectively (table 1). Thus, more than twice as many were made during the second as the first period (t = 6.38, P = 0.0007). The average number of PMFs per colony on both buildings in the spring (1.76) did not differ significantly from that (1.98) in the second autumn period (t = 1.20, P = 0.28). Thus, except for the first autumn period, about two PMFs per colony were performed during the rest of the season. However, it should be noted that more PMFs per colony were made during the three days at the end of November and in December (2.13) than during the three spring days (t = 9.17, P < 0.001).

No significant correlation was found between the number of PMFs per colony and average daily air temperature (r = –0.25, df = 12, P = 0.40).

The highest percentage of colonies performing PMFs and the highest number of PMFs per colony were performed in December at the time when the largest amount of brood was present in the colonies.

Percentage of colonies performing different number of periodic mass flights

Particular colonies performed between zero and six PMFs per day throughout the total period of observations (tables 1 and 2).

Two PMFs, at least, were performed by 22% of colonies during the first autumn period, and by about three times as many (60%), during the second period (t = 4.12, P = 0.006). A similar percentage of colonies (54%) performed two PMFs in the spring (t = 0.43, P = 0.69). Thus, with the exception of the first autumn period, roughly 55% of colonies performed at least two PMFs.

Three PMFs (at least) were performed only twice during the first autumn period; 28% of colonies performed such flights during the second period, and 19% in the spring. (These last two means did not differ significantly t = 1.24, P = 0.27). Thus, except for the first autumn period, workers from about 25% of colonies performed at last three PMFs.

Four PMFs, at least, were performed by 9% of colonies only during the second autumn period. Five PMFs were made only during two days, and six flights during one day in the second autumn period when the largest amount of brood was present in the colonies.

Duration and diurnal distribution of periodic mass flights in different seasonal meteorological conditions

With the progress of the season, the autumn daily average temperature decreased by 8.6 °C and the spring temperature increased by 8.8 °C (tables 1 and 2).

The distribution of all PMFs performed at different times of the day differed on various days (fig. 1). During the coldest day (14 December, average18.9 °C), PMFs were performed within a short range of 5 h. Most flights were performed at midday. During slightly warmer conditions, both in autumn and spring (25 October, average 26.2 °C and 25 March, 28.0 °C), the time range of flight was extended to seven or nine hours. However, in these conditions, a one hour gap with no PMF occurred at midday. During the hottest conditions (2 April, average 33.6 °C) PMFs were performed over 11 h with a long gap of six hours during which there was no PMF. Thus, at low average daily temperatures one peak of PMF activity occurred at midday, whereas at high average daily temperatures a bimodal distribution was observed.

PMFs were not observed under temperatures below 17–18 °C, or in foggy or partially/fully cloudy days (8 November and 8 December).

A highly significant correlation was found between the duration of PMF activity and average daily temperatures in both seasons treated separately, as well as in all sunny autumn and spring days treated together ($r = 0.93$, df = 11, $P = 0.0000$). Regression analysis showed that an increase of average daily temperature by 1 °C was associated with a 24-min increase in the duration of PMF activity.

A significant correlation was found in autumn and spring between the duration of the gap with no PMF and average daily temperature ($r = 0.98$, df = 5, $P = 0.0007$).

The distribution of PMF activity in autumn and spring was similar at similar average daily temperatures (fig. 1, cool days: 15 November, average 23.7 °C and 5 March, 24.8 °C, $Ex = 8.91$, df = 6, $P = 0.176$, $n = 75$; warm days: 25 October 26.0 °C and 25 March, 28.0 °C, $Ex = 9.19$, df = 7, $P = 0.226$, $n = 42$).

The distribution of PMF activity in two populations at two buildings was similar the same days (25 March, $Ex = 1.60$, df = 7, $P = 0.987$, $n = 42$; 2 April, $Ex = 1.27$, df = 4, $P = 0.978$, $n = 41$).

Thus, the pattern of PMF activity was correlated with average daily temperature.

Relation between day length and the length of PMF activity

Day length decreased in autumn by 1 h 5 min and in the spring it increased by 45 min (fig.1).

In autumn, decrease of the duration of PMF activity was correlated with the decrease of day length ($r = 0.88$, df = 6, $P = 0.0095$). However, day length and PMF activity did not decrease by the same time length. While day length decreased by only 1 h 5 min, PMF activity did so by as much as 5 h. Regression analysis showed that decrease of day length by 1 h in autumn was associated with a 3 h decrease of PMF activity. In the spring, increase of the duration PMF activity was correlated with an increase in day length ($r = 0.88$, df = 4, $P = 0.0461$). However, while day length increased by only 45 min, PMF activity did so by as much as 4 h. Regression analysis showed that increase of day length by 1 h in spring corresponded to a 4 h 34 min increase of PMF activity.

Correlation between duration of PMF activity and day length during the total period of observation was $r = 0.88$, df = 11, $P = 0.0001$.

However, average daily temperature was also correlated with duration of PMF activity ($r = 0.93$) and explained more of the variability ($R = 85.8\%$) than did day length ($r = 0.88$ and $R = 77.8\%$).

Frequency distribution of consecutive periodic mass flights during the day

The question is whether first PMFs were performed in the morning and subsequent ones in the afternoon.

During the period from 1 November until 20 December and again at 5 March, unimodal frequency distributions of PMFs were observed (fig. 1). Workers of some colonies made their first PMFs in the morning as well as the afternoon. Second PMFs were performed while other colonies had not yet made their first. Third flights were made at the same time at which workers of other colonies were performing their first or second flights. Thus, it was not the case that first PMFs were made in the morning and subsequent ones in the afternoon.

During warm and hot meteorological conditions on 18 and 25 October, 25 March, and 2 April, bimodal distributions occurred with gaps of no flight (fig. 1). Colonies made first PMFs before the gap as well as after it. Some made second flights earlier, or at the same time at which others made their first flights. Hence, the bimodal distribution was not caused by first PMFs being made before the gap and others after it.

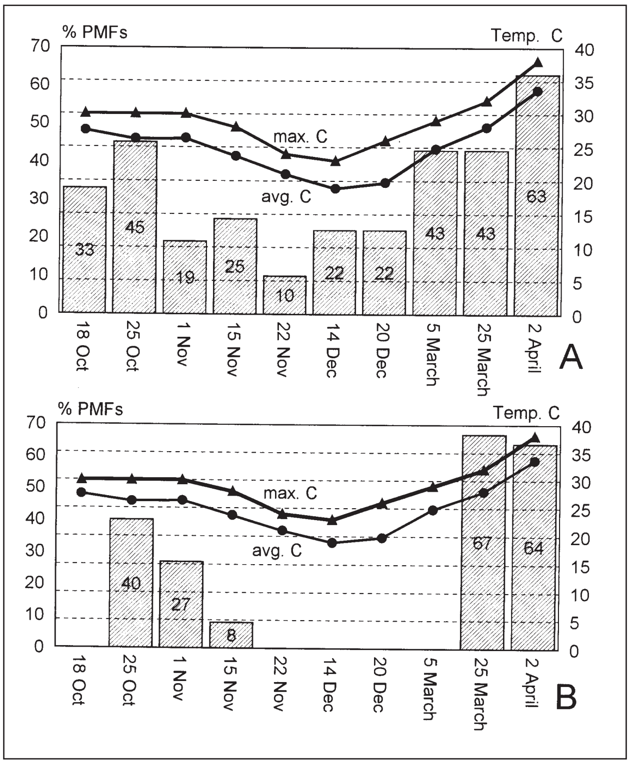

FIG. 2. Percentage of periodic mass flights (PMFs) activities performed after the maximal daily temperature at 14:00 h. A – PMFs of all colonies, B – PMFs of colonies which performed exclusively one flight per day. Curves: max. C – maximal daily temperature, avg. C – average daily temperature.

Maximal daily temperature occurred around 14.00h. At days with higher temperatures (daily average and maximum, fig. 2A), the percentage of PMF activities performed after the hottest time of day increased significantly from 10% to 63%, ($r_{avg} = 0.80$, $P = 0.006$, $R = 63.3\%$ and $r_{max} = 0.84$, $P = 0.002$, $R = 70.9\%$).

Colonies performing exclusively one PMF activity per day were also tested. At days with lower temperatures no PMFs were performed after the daily maximum temperature of 24–29 °C (fig. 2B). However, on days with the highest temperatures as many as 64–67% of PMF activities were performed after the maximal temperature of 32–38 °C ($r_{avg} = 0.75$, $P = 0.012$, $R = 56.9\%$ and $r_{max} = 0.78$, $P = 0{,}007$, $R = 61.4\%$).

In both cases (all PMFs or exclusively 1 PMF per day), maximum ambient temperature was closely correlated with the percentage of PMF activities performed after the hottest time of the day and explained more variability than did average daily temperature.

In summary, the tendency to perform PMF activities after the highest daily temperature was more pronounced on warmer than cooler days.

DISCUSSION

Until now, observations were reported for only a few days on 17–33 PMF activities (Mardan & Kevan, 1989) or on 15 activities (Kastberger *et al.*, 1996). In contrast, we have observed 410 PMF activities for up to 48 colonies over a period of several months. This helps us to describe different characteristics of PMFs and discriminate which depend on environmental conditions and which upon the development stage of the nests.

We found that the air temperature alone was not the factor determining either the percentage of colonies performing PMFs or the number of flights per colony.

Instead, we observed the highest PMF activity at the time of maximal development of the colonies. Hence, we suggest that the percentage of colonies performing PMFs and number of flights per colony depend on the status of the colonies, including such factors as amount of brood and number of emerging workers. This can be explained by the requirement for larger amounts of larval food in stronger colonies. Higher numbers of young nurse bees, which produce more larval food, also produce more faeces which is expelled during PMFs.

However, the diurnal frequency distribution of PMF activities, daily duration of all PMF activities, as well as duration of the gap between morning and afternoon activity were correlated with ambient air temperature.

The PMF activity was short, about 5 min. During that activity, disorder of the nest curtain occurred, sometimes to the extent that comb was partially exposed (Muthuraman & Srinivasan, 2002). A protective thermal function of the curtain, especially against low (18 °C) and high (36–38 °C) temperatures, could not be verified. Nevertheless, we suggest that the short duration of PMF activity is a strategy to minimize disruptions to the curtain and colony thermoregulation.

One of the important results is the finding of one peak of PMF activity at lower ambient temperatures and two peaks at higher ambient temperatures. The midday peak of PMF frequency distribution we observed at lower ambient temperatures has not been reported by other authors. However, bimodal distribution at higher temperature was observed. According to Mardan & Kevan (1989), out of 17 PMFs performed at 29.5 °C ambient, 60% were made before noon and 20% after. This is similar to the distribution of 78% and 22% PMFs we observed at 27.5 °C average daily temperature. Kastberger *et al.* (1996) recorded PMFs performed in warm conditions also in two separated periods: before and after noon.

Attempts to explain the pattern of uni- or bimodal PMF distribution were not undertaken. We suggest that bees perform the different patterns of PMFs to prevent the negative effects of curtain disorder and comb exposure and, by extension, colony thermoregulation. At low ambient temperatures the bees perform PMFs around midday when the ambient temperature is highest to prevent cooling the nest, which would happen if flights were performed during cool (18 °C) morning and afternoon hours. In contrast, at high ambient temperatures the bees perform PMFs in the cooler morning and afternoon hours to prevent overheating the nest, which could happen at the highest (36–38 °C) midday temperatures.

Apis dorsata workers perform PMFs at higher ambient temperatures (> 17 °C) than do *Apis laboriosa* workers (> 11 °C, Woyke *et al.*, 2003). This is an adaptation to environmental conditions. However, only one midday peak of frequency distribution of PMFs occurs in both species at average daily temperature below 22 °C. This agrees with the above explanation.

Workers returning from a PMF landed over the entire surface of the curtain and not at the mouth zone as reported by Kastberger *et al.* (1996). This difference may be due to observations made on the curtain surface facing a window rather than the outside surface to which landing workers had free access.

Mardan & Kevan (1989) and Mardan & Ashaari (1990) suggested that mass flight and defecation occur when thermal stress is greatest. It can help avoid nest temperatures reaching a lethal level of about 37 or 38 °C. However, during our observations air temperature generally did not exceed 32 °C. Thus, it is not likely that defecation was being employed in this manner under our conditions. During the warmest days, as many as 63% of all PMFs activities were performed after the hottest period of the day. Colonies which performed exclusively one PMF activity per day made as many as 67% of them after the highest daily temperature. Defecation during those late PMFs could not serve to avoid lethal temperatures occurring during earlier, hotter midday hours. Thus, defecation-mediated thermoregulation can constitute only part of the function of PMFs.

During our observations, drops of faeces fell on us only sporadically. No shower of yellow rain occurred. The low density of faeces on the nearby vegetation agrees with Seeley *et al.* (1985) that density of spots is low directly under nests and up to about 20 m.

Kastberger *et al.* (1996) suggested that PMFs are performed for orientation of young bees, defecation and change of worker bee position in the curtain. Our observations support the view that PMFs serve for orientation and defecation of young workers.

In summary, we suggest that both the short duration of PMF activity (*c.* 5 min) as well as diurnal patterns of PMFs (one midday peak, or two; one in the morning and one in the afternoon) are strategies to minimize disruption of the protective bee curtain and consequent compromises to colony thermoregulation.

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Periodic mass flights of Apis dorsata are available online at:
http://www.sggw.waw.pl/~woyke/21DoPMF1.avi
http://www.sggw.waw.pl/~woyke/22DoPMFZ.avi