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Original article

Behavioural features of a periodic form of massed flight activity in the giant honeybee *Apis dorsata*

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Summary — A periodic form of massed flight behaviour in *Apis dorsata* was studied by video recording and image analysis. Two to three times a day the nest turns from the quiescent state into a high level of commotion for about 5 min. The vertical body orientations of the bees in the curtain then become more and more 'disordered'. In one nest, the total percentage of bees which flew off was less than 20% and the maximum number of hovering bees at a moment was 2–3% of the bee colony. Half of the curtain bees in the surface layer changed their position. The median moving index was below 0.3 mm/s in the quiescent condition and it rose up to 1.0 mm/s during massed flight activity. Our observations indicate that this kind of massed flight is quite different from the great defecation activities reported previously. Although there are diverse forms of massed flight activities in *A dorsata*, we found that this form of massed flight actitivity causes the periodical rearrangement of the roofing layer of curtain. On a Banyan tree we counted more than 100 nests of *A dorsata* and observed that nests of different areas of the tree did not supply bees or mass activity simultaneously.

***Apis dorsata* / massed flight activity / orientation flight / image analysis / India**

INTRODUCTION

The Asian giant honeybee *Apis dorsata* Fabricius, 1798 is known to nest in the open. The nests are suspended from tall trees, buildings or cliffs reaching sometimes 1.5 m in the horizontal span and comprising up to 60 000 individuals (Ruttner, 1988). Massed flight activities represent an important feature of its social behaviour. The significance of this behaviour for the colony, however, is not fully known, especially as there may be several types of massed flight activity. A striking form of massed flight with nearly half the nest involved has been reported (Seeley et al, 1985) and was linked with defecation and temperature regulation in the nest (Mardan and Kevan, 1989; Mardan and Ashaari, 1990). In fact, defecation can be quite spectacular and under the name 'yellow rain' was misinterpreted as a kind of biological warfare agent by the US state department (Ember, 1984; Maddox, 1984; Seeley et al, 1985). However, massed flight in *A dorsata* might also occur in defense (Koeniger, 1975; Veith et al, 1978), in seasonal migration (Koeniger and Koeniger, 1980), during swarming (Lindauer, 1956) and during drone flight (Koeniger and Wijayagunasekera, 1976; Koeniger et al, 1994).

We investigated a periodic form of massed flight behaviour in *A dorsata* which might be homologous to the well-known 'playing about' during orientation and cleansing flights in *Apis mellifera* (Stadler, 1911; Rösch, 1925; Becker, 1958; Von Frisch, 1967).

MATERIALS AND METHODS

Observation sites

Nests of *A dorsata* were found in the campus of Jawarharlal Nehru University (JNU), New Delhi suspended from various buildings. We observed three nests outside the window of a laboratory during the period of July, October and November 1994 and November 1995. The nests were oriented with one side (inner side) to the wall of the building and with the outer side (outer side) facing east. In the course of a day the inner side remained shady ('shadyside') whereas the outer one ('sunny side') received direct sun from sunrise (0630 hours) to the early afternoon (1300 hours).

The nest we observed in 1995 spanned 80 x 70 cm (width x height) and was 15–20 cm thick which allows us to estimate 4–6 layers of curtain bees (assuming 1 cm for each layer). The bees were counted in a central area on the surface of the inner side of the nest; the number of individuals, extrapolated for one layer and further for the whole nest, were estimated to be 25-30.000 individuals (22 400, 28 000 and 33 600 for 4, 5 and 6 layers, respectively) in the nest.

In November 1994 and 1995 days were generally sunny without any clouds. The temperature was about 22 °C in the morning, during the day it rose to 30 °C, and in the night it did not fall below 20 °C.

A dorsata nests were also observed in Assam, near Kaziranga National Park, where more than 100 nests were suspended from the limbs of two Banyan trees *(Ficus bengalensis)*. The temperature in Assam (November 1995) was higher than in Delhi, above 30 °C during the whole day at 70–80% relative humidity. With the camcorder we recorded the activities of the bees from the ground for 6 h.

A third observation was made near Chitwan National Park in Nepal at the end of spring in April 1996 where eight colonies of *A dorsata* were found hanging from a Banyan tree. At this time the maximum temperature was 38 °C.

Recording and analysis of video data

We filmed the nests in JNU simultaneously with two cameras (fig 1). One camera (c1) recorded the nest activity at the outer sunny side or at the inner shady side, the other one (c2) was directed into the air near the nest to document the number of bees coming out, arrival and hovering. The video films were examined by image analyzing methods using the OPTIMAS software package. The behaviour of bees in and around the nest was assessed by the following parameters. The number of bees flying near the nest was counted in the minutes before, during and after massed flight activity. For that purpose we defined a rectangular sample area (sa2 in fig 1) measuring 120 x 100 cm. This area represented a volume of several cubic meters making up one third to a quarter of the region around the nest where massed flight activity occurred. Every second we assessed the number of flying bees in this sample area in one frame. This time interval of 1 s was suitable to ensure that different bees were recorded in successive frames (number of bees evaluated: 14 483, number of frames: 246). To quantify the behavioural aspects at the shady side of the nest we assessed the orientation of the surface bees by the angle of each bee's long axis. We defined the angle of the bees hanging with their heads pointed upwards and directly away from the ground as 0°. With the help of camera c1 we counted all departures and arrivals at the surface of the inner side of the nest, the recordings with camera c2 provided the basis for counting the departures and arrivals from the whole nest, and enabled us to trace the flight paths of individual bees hovering in the cloud near the nest. Slight movements of curtain bees were evaluated by a moving index which considers the horizontal (Δx) and vertical (Δy) offsets of the frontal and caudal confines of the single individuals between two frames ($k-1$, k), successively evaluated in steps of 10 s according to

$$\Delta x = (x_k - x_{k-1}) \text{ and } \Delta y = (y_k - y_{k-1}) \quad [1]$$

$$v = \mathrm{ABS}(\sqrt{(\Delta x^2 + \Delta y^2)} / s) \text{ [mm/s]} \quad [2]$$

$$\text{Moving index} = v_{frontal} + v_{caudal} \text{ [mm/s]} \quad [3]$$

RESULTS

The 'quiescent' nest condition

The bees forming the protective curtain at both sides of the nest (the sunny and shady side) remained motionless most of the time (fig 2a). The individual bees of the curtain hung upwards, wings spread, with a slight inclination towards the comb-like roofing tiles, with the head covered by the bee above and the abdomen exposed. This observation is consistent with previously reported data (Ruttner, 1988).

An active area, the 'mouth' of the colony (Morse and Laigo, 1969), was located in the lower part of the curtain, exclusively at the sunny side. Here, the orientation of individual bees was irregular, the heads were frequently directed outward. Activities like dancing, social feeding, departure and arrival were observed throughout the day at this region. In the first hours after sunrise, this 'mouth' zone extended to the upper region of the nest.

Colonies exhibiting these conditions were termed 'quiescent'. Colonies were quiescent except during periods of 'massed flight' (see below).

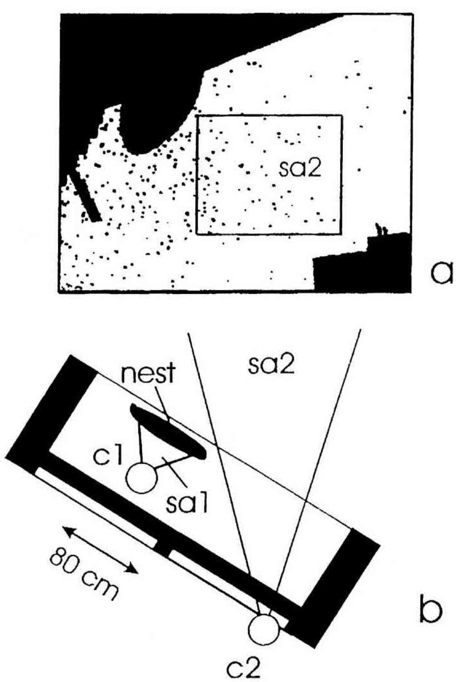


Fig 1. a) View of the nest in JNU during massed flight activity; **b)** ground view of observation setup: the nest had a width of 80 cm; c1, camera for filming the central part of the shady side of the nest (sa1, sample area 1); c2, camera for filming the nest and its surroundings; measurement of flight rate referred to sample area 2 (sa2, see also the rectangular field in **a**).

The 'massed flight' condition

Two to five times a day the activity of the colony dramatically increased for a short period. We noticed this behavioural contrast in particular at the less busy, shady side of the nest. The previously motionless curtain bees began to wag slightly, changing their position and their orientation, and within 1 min the regular display of the nest seemed to be in complete disorder (fig 2b). The number of bees hovering around the nest increased quickly, and then decreased over a short period until bees were again quiescent.

We observed massed flight activity at the nest in JNU campus over three weeks. Observations made at irregular intervals over one a year period (Biswas S, unpublished data) reveal that these periodic events are a regular phenomenon. We observed,

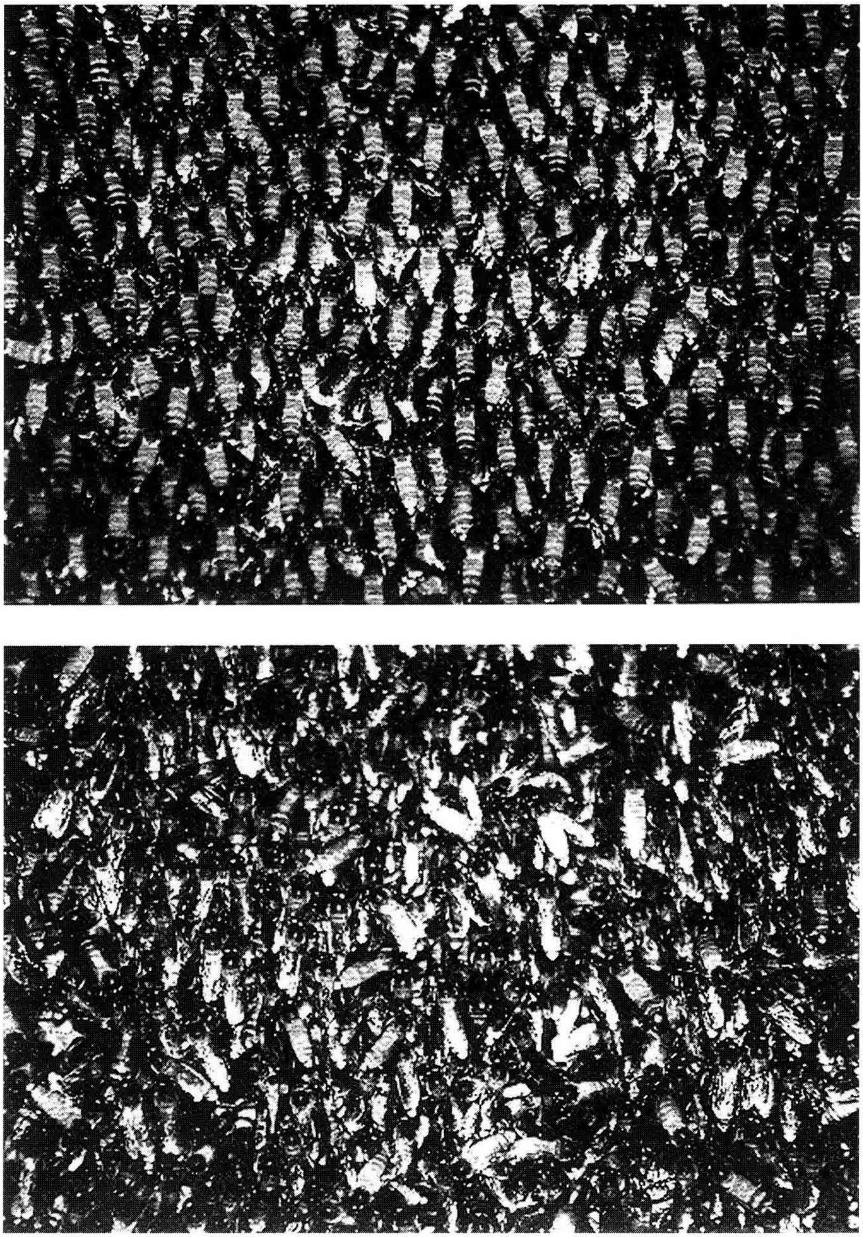


Fig 2. Display of curtain bees at the center of the shady side of the nest. Top: quiescent behaviour of curtain bees hanging vertically in parallel; bottom: during massed flight the center of the shady side turns into a busy region where bees run over each other. Here was also the center for departure from the shady side.

strong massed flight activity between 0900 and 1100 hours. The massed flight period in the afternoon between 1300–1500 hours was weaker, and that in the dusk between 1745 and 1800 hours was slight. However, in November 1994 all the massed flight activities we observed were more extensive, probably due to the larger size of the nest at this time.

One massed flight period in detail

The following analysis refers to a single massed flight activity observed on 9 November 1995 before midday. The video recording of the nest (c2 in fig 1) was taken for 30 s every 5 min from 0830 to 1042 hours, continuous filming with two cameras (c1,c2) was performed between 1042 and 1110 hours.

Features of periodic massed flight activity around the nest

Massed flight activity lasted less than 6 min (from 1042 to 1048 hours) and was indicated by an increased rate of bees hovering around the nest. Within 1 min the number of bees flying around the nest increased from the background quiescent level of 0–3 bees / frame to about 50 bees / frame in the sample volume *sa2* (fig 3a). In the following minute the flight activity reached its maximum with 200 bees/frame. In the following 4 min the rate declined again to the quiescent condition. The sample volume sa2 represented a third to a quarter of the whole area around the nest from which we estimate that the maximum number of hovering bees was 600–800. Considering the number of bees in the nest (25 000, see *Materials and methods*), the maximum number of bees hovering around the nest at the highest level of massed flight activity was not more than 2–3% of the colony.

The rate of bees flying off during the given massed flight activity was determined in detail only for the shady side of the nest. Here, the rate of bees increased from 0 to 25 bees per second within 1 min and decreased again to zero in the successive 3 min (fig 3c). These data are temporally consistent with the increase and decrease of the number of hovering bees (fig 3a). In 5 min we assessed 1 905 departures (fig 3c) and 150 arrivals (fig 3d) on the shady side. The maximum rate of the bees departing from the shady side of the nest was less than 25 bees per second (fig 2c). However, in the video recording from the whole nest (c2) we have assessed the maximum total rate of bees departing the nest at 60–80 bees per second. Therefore, total bees departing from the sunny side of the nest can be calculated to be two to three times the number of bees having started from the shady side. Therefore we estimate that at least 6 000 individuals or some more than 20% of the bee colony had left the nest during the massed flight period observed here in detail.

The special distribution of bees flying in the sample area sa2 (fig 3a) indicated that bees joined the hovering cloud in several steps. To analyze the origin of these bees we traced characteristic flights of around 50 bees that had just left the nest. Eighty percent crossed the sample volume sa2, encircled around the nest and disappeared from the image within 2 s, 20% landed again on the nest after only one round. A certain number of hovering bees set out for arrival especially at the rim areas of the sunny nest side.

The bees that flew off returned and remained near the nest, hovering in gentle arcs. From outside the building below the nest we could observe that during this flight activity most of the bees did not fly further than 20 m. The arrival rate of bees was not increased in the next hour after the massed flight period. In consideration of the total number of bees flying off (6 000 bees) and the maximum number of bees hovering at a given moment (600–800 bees) we can con-

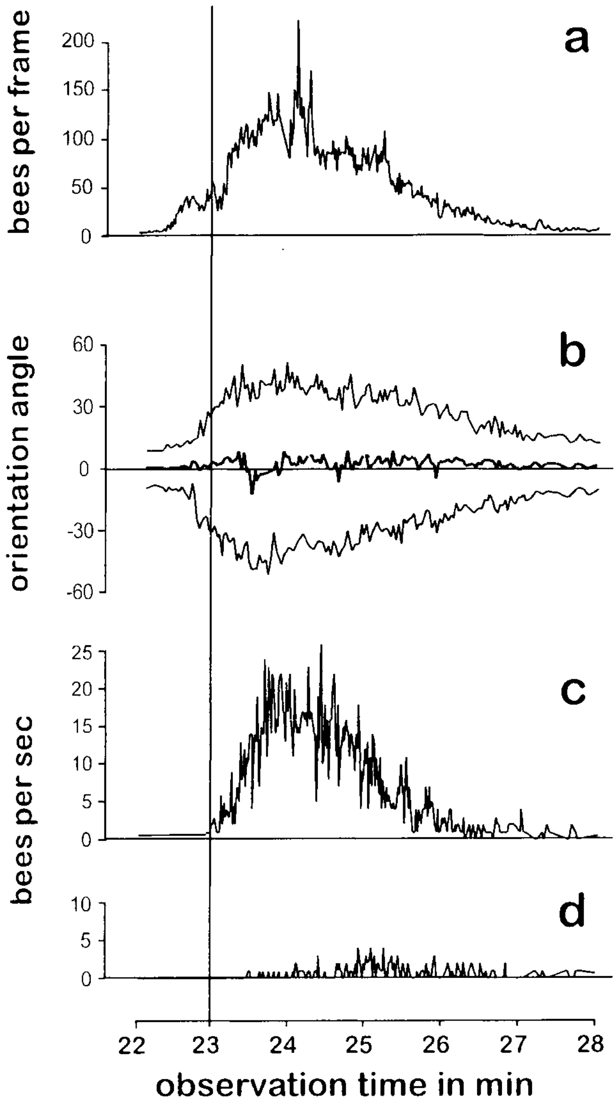


Fig 3. Massed flight activity at the nest in JNU on 9/11/1995 before midday; measurements are taken before, during and after this activity period; the curves represent different behavioural parameters and refer to the period between 1042–1048 hours when the nest was continuously filmed with camera c1 and c2 (see fig 1): **a)** the number of bees which have been detected in the sample region near the nest filmed with c2, measurements have been taken per frame every second (total: 14 483 bees in 329 frames); **b)** the distribution of the orientation angle of the surface bees per frame every 2 s (total: 93 190 bees in 246 frames) at the shady side of the nest in the sample area detected by c1; 0° refers to the vertical direction of the body's longitudinal axis of quiescent curtain bees with their heads pointed straight up; middle curve gives the median direction, the lower and upper curves give the 25 and 75% values of the distributions; **c)** the number of bees (total: 1 905) which have started from the sample area sa1 of the shady side of the nest; **d)** the number of bees (total: 150) which have landed on sa1.

clude that most of the bees stayed off the nest for only a part of the massed flight period. These data also prove that the majority of the individuals having flown off from the shady side must have landed on other areas of the nest during the massed activity.

Features of massed activity at the nest itself

The massed acitivity period we observed in detail started shortly after 1042 hours. In particular on the shady side we observed how bees emerged to the surface of the curtain. They crawled out through the motionless hanging curtain bees and assembled themselves in the center of the shady side forming a cluster (fig 2b). A second group of bees came from the rim zones and added to this cluster in the center of the shady side. A third group of bees participating in mass activity came from the surface layer of the curtain itself. These bees moved their abdomen first, shifted the whole body and crawled like other active bees to the middle of the nest. However, we did not observe any bee, participating in massed flight, which originated from the curtain just below the roofing layer. Most of the cluster bees flew off (fig 4).

Furthermore, we quantified the movements of 400–700 surface bees at the shady side by assessing position and orientation every 2 s. We found that the median direction of the body's longitudinal axis was vertical around 0° throughout the massed flight period (fig 3b), although the half of the sorted data (from the first to the third quartile) ranged from –50° to +50°. This expresses 'disorder' in the nest, a clear contrast to the otherwise regular display of the quiescent nest condition.

To quantify the number of moving bees we evaluated position and posture of individual bees from the surface layer before and after the activity period (fig 5) and traced them in the video film by playing it in forward or reverse mode. Therefore, we analyzed 162 individuals (1 812 measurements) on the shady side and assessed their moving index (see *Materials and methods*) to detect fine movements of the bees. Thirty- eight out of 76 curtain bees hanging quiescently in the surface layer flew away during mass activity, and 39 out of 86 bees that were observed to form part of the surface layer after the massed flight period came from somewhere else. The median moving index was at 0.3 mm/s in the quiescent condition and rose up to nearly 1.0 mm/s during mass activity. This is caused by two effects: some bees reached velocities of more than 1.0 cm/s, and a significant number of non-walking bees started to move only slightly or were pushed around by the walking bees. As a consequence, the velocities of the bees (fig 5) are distributed non-linearly, in contrast with the distribution of their orientation (fig 3b).

Observations on a 'bee tree'

On the limbs of a Banyan tree in Assam we counted more than 100 nests of *A dorsata*. At least 40 of them spanned 1.30 m in width and 0.80 m in height with approximately double the size of the nest in JNU we had experimented with. The nests were arranged with a space of only one meter or less between them (fig 6). On two days (23 and 24 of November 1995) we observed 15 episodes of massed flights in 8 h. Similar to the observations in Delhi, massed flight periods lasted only for several minutes each. We did not observe that nests of different areas of the tree supplied bees for mass activity simultaneously. We think that only a certain nest in a particular branch area showed it in a certain period. Only once in 6 h we observed massed flight activities at two nests of the tree at the same time. However, these two activity centers were 20 m apart. By video records and photographs it was possible to relate the cloud of bees to the nest of origin because of the density gradient of hovering bees and the limited

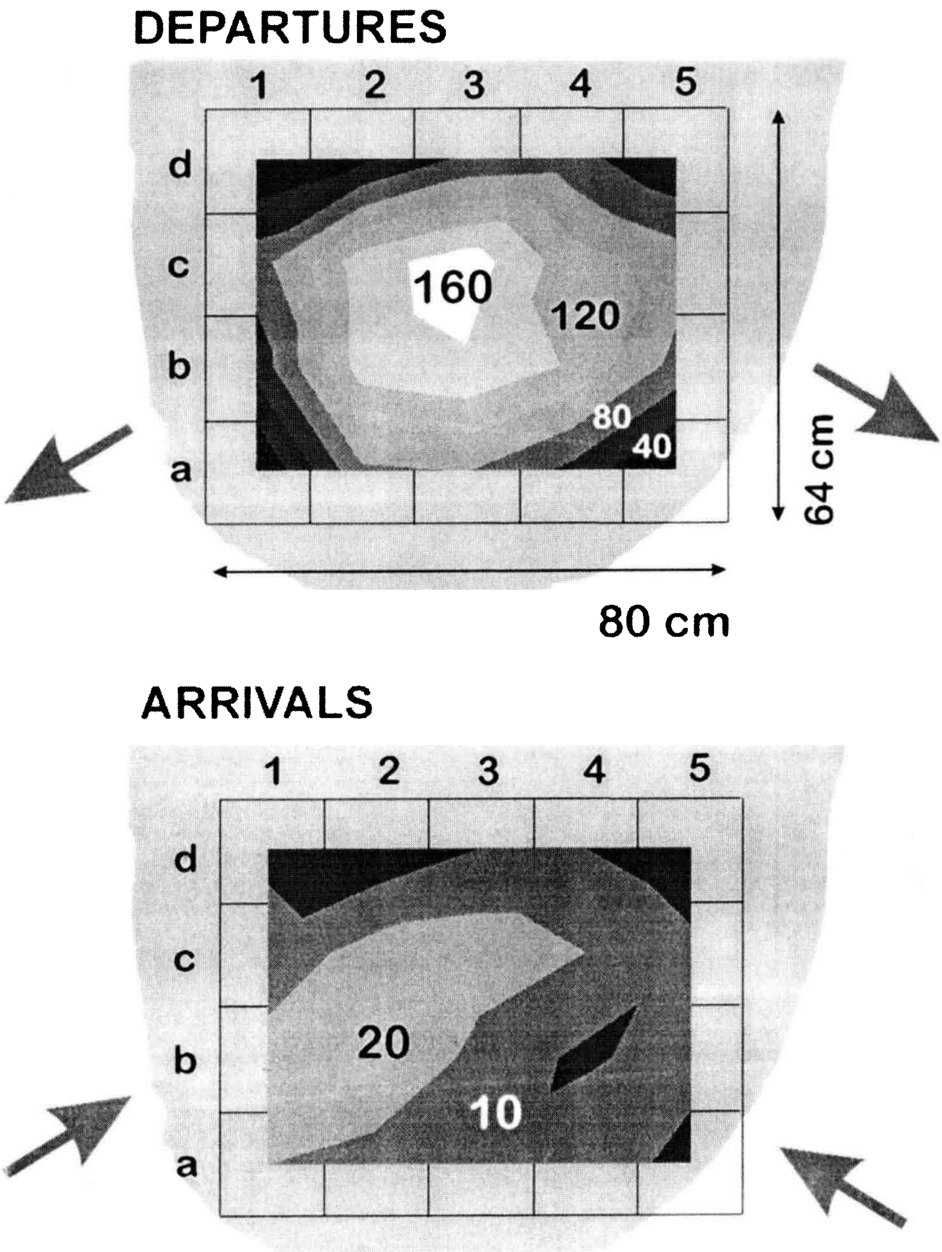


Fig 4. Display of rate gradients of departures and arrivals from/to the shady side of the nest. The departures and arrivals had been traced for 20 areas (1a–5d) in the sample field, measuring 80 x 64 cm. Numbers in the field give the numbers of departures / arrivals during the observation period (see fig 3).

extension of the cloud of the bees. Figure 6a shows one of those massed flights in an area of the tree with about ten nests in direct vicinity. A projected number of 10 000 bees flew around and there was an unmistakable density gradient of the bees in relation to the nest which was situated outside the left border of figure 6a. However, we do not

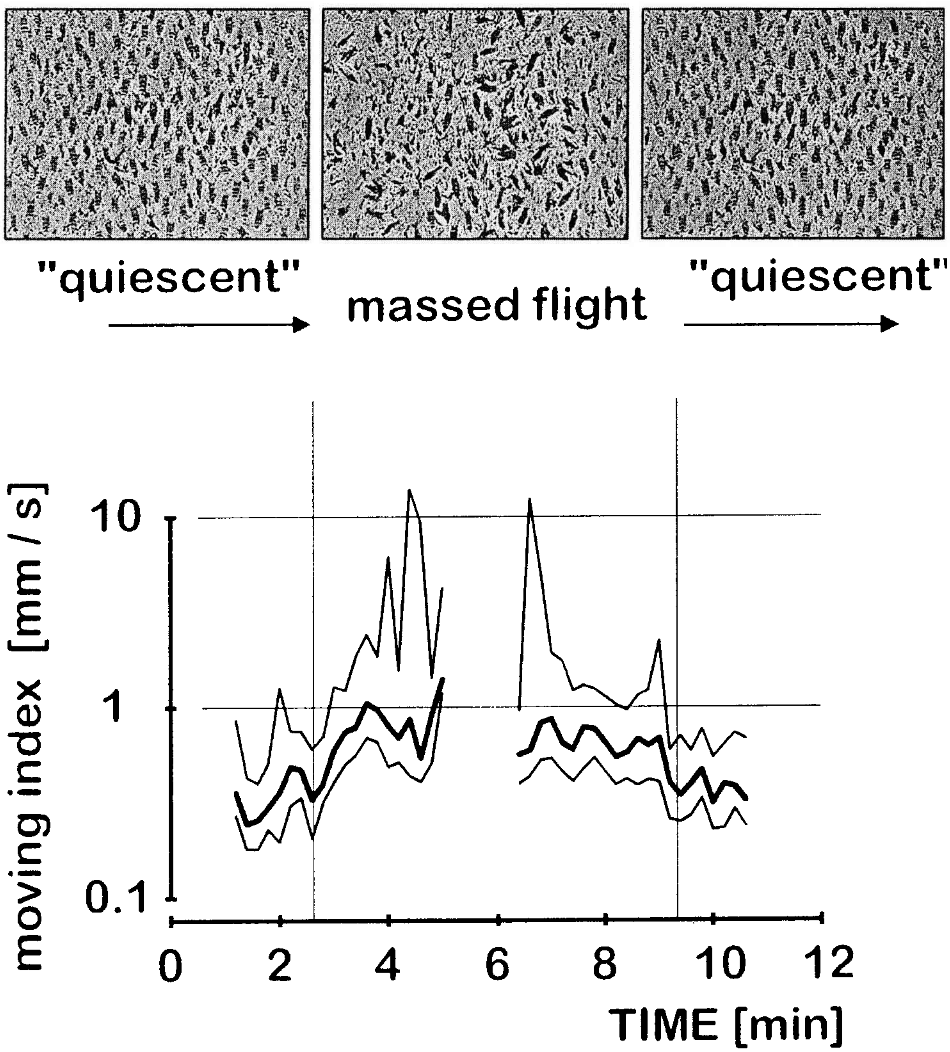
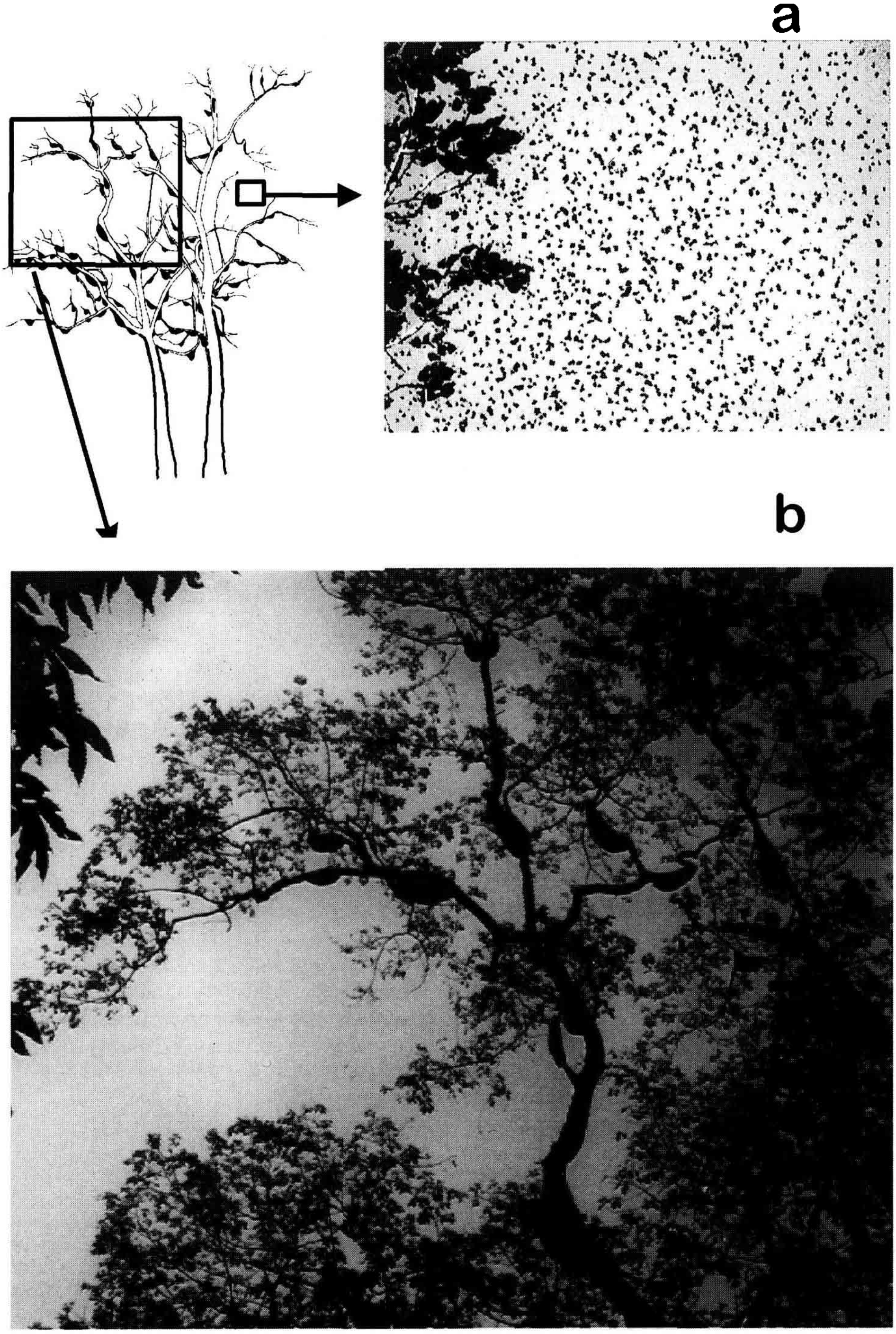


Fig 5. Moving index of curtain bees at the surface layer on the *shady* side. The left curves give median, 25 and 75% values of the distribution of curtain bees before massed flight activity had started. The curves on the right side refer to surface bees which had gone off and come to the place where they become 'motionless' quiescent curtain bees. During maximum activity the continuous measurement of the moving index of bees in the surface layer was not possible because of the mass of overrunning bees. Data were assessed every 10 s from 20 individuals per frame (total: 167 individual bees, 1 800 measurements). For contrastful display the gray tones of the images had been inverted.


a
b

know for sure whether the bees had also come from other nests nearby. If only a single nest was forming the cloud and if the nest had 60 000 individuals, the number of the bees in the cloud was about 20% of its population.

DISCUSSION

The number of bees in massed flight

In the relatively small and single nest in JNU only 2–3% of bees were hovering around the nest at a particular time, but in total 20% of the colony participated in massed flight in the course of 5 min. On the tree in Assam we counted about 10 000 bees (which could be 20% of a single big colony) hovering at some spots at different points of time. We consider both massed flight activities as similar phenomenon. Possible causes influencing the dimension of massed activity are the size of the nests, the amount of brood cells, the number of colonies at one site or even the contribution of nearby nests to the cloud of hovering bees.

There are some reports that assume that more than 20% bees of the colony participate in massed flight. According to Mardan and Kevan (1989) half of the nests were active during massed flight. Seeley et al (1985) described an area with a hundred thousand yellow defecation spots, which had come from one shower of yellow rain. However, it is unknown how many defecation spots were caused by a single bee, and which kind of swarmlike activity had happened (migration, defense attacks, proper swarming, etc). In Nepal we also found (in April 1996) enormous amounts of yellow spots (1 000 per m^2) accumulated at a distance of 30 m from the nests of *A dorsata*. We assume that these yellow spots originated from the defecation activity of the bees during daily cleansing flights in the course of several weeks.

Temperature does not trigger periodic massed flight activity

The nests we observed at JNU were positioned in such a way that they received the first rays of the sun and were under shadow after midday. Each day, the first massed flight activity occurred under sunny, very bright and warm conditions of 35 °C. A second period of activity happened under shady conditions of 28 °C in the afternoon (the third at dusk is probably related to drone flight and to mating activity, see below). Even in the warmest monsoon month in Delhi (in July 1994 at 48 °C and high humidity rate) massed flight behaviour happened periodically and the intensity and duration was similar to that in November.

These facts indicate that massed flight activity in *A dorsata,* which we call 'periodic', is neither primarily determined by ecological factors (like illumination or temperature) nor by seasonal factors (like dry or rainy period or mating season). From the observation of the nests on a Banyan tree in Assam (see fig 6) we come to a similar conclusion. The massed flight activities occurred successively at different sites of the tree. If the temperature is the dominant factor for inducing massed flight, it is expected that some or many neighbouring nests of that tree would have swarmed together.

Fig 6. The Banyon tree in Assam near Kaziranga on 23/11/1995 with more than 100 nests. Massed activity was viewed **(a)** in an area on the right side of the tree, measuring 1.5 x 1.0 m; **b)** shows the upper left region of the tree with more than 20 colonies.

In contrast, Mardan and Kevan (1989) suggested that thermal stress for the larvae could be the primary factor for massed flight. They calculated that the heat loss of the nest by the defecation of a mass of bees would be essential for thermoregulation.

On the other hand, temperature of brooding site might be indirectly regulated through massed flight activity in two ways: (1) by thinning out the nest which enables proper ventilation; or (2) through evaporative cooling (gobletting), which Mardan and Kevan (1989) had observed before and even after massed flight.

Biological role of massed flight behaviour

Periodic massed flights observed in *A dorsata* are not yet completely understood but they probably serve several functions. First, they resemble the orientation flights of young *A mellifera* (Stadler, 1911; Rösch, 1925; Becker, 1958; Von Frisch, 1967), where at midday in the sunny summer season young bees of varied age groups (5–13 days) form dense masses in front of the hive (Rösch, 1925). During such orientation flights the bees gain information about landmarks and the location of the hive (Rösch, 1925; Von Frisch, 1967; Michener, 1974; Lehrer, 1993). The duration of activity in *A mellifera* may last up to half an hour; single bees, however, return after a few minutes (Becker, 1958; Von Frisch, 1967).

Second, defecation is another aspect of massed flight. In *A mellifera*, young bees in their first few days clean brood cells, eat stored pollen and nurse the brood. During this time pollen accumulates in their recta. Borchert (1966) assumed that the young bees would be ready for their first flight if the content of their rectum exceeded a quarter of their body weight. Cold and rainy weather or low temperature in wintertime hinders them to leave the hive to void their feces. In fact, the increased flight activity observed after such periods has been called 'cleansing flights'.

Massed defecations of *A dorsata* have been described as 'yellow rain' (Ashton et al, 1983; Nowicke and Meselson, 1984; Seeley et al, 1985) and might be caused by circumstances similar to that which evoke the cleansing flights (Rösch, 1925) of the honeybees in temperate zones. For example, monsoon rainfall can be so heavy and long-lasting that the bees have to stay in the nest for several days, waiting for the first warm day. Similarly, temperature might be an important precondition to perform massed 'cleansing flights' in *A dorsata*. In the mountains of the Westghats in southwest India we have observed (in 1990) an migrating *A dorsata* swarm that was suspended from the branches of a bush. At a temperature of 15 °C the bees were immobile and the colony, caught by the cold weather, had to wait for the next sunny day to continue migration.

One possible consequence of the kind of massed flight activity we observed is that the structure of the bee curtain is periodically changed in a certain order. At least two further aspects are of interest. First, only during massed flight activity did we observe bees emerging from lower levels of the curtain to the surface through the roofing bees. This also happened far away from the 'mouth' zone. We assume that these bees represent young ones which have gone through the sequence of jobs of the first 7–10 days of their life (Rösch, 1925; Otis et al, 1990; Seeley, 1995) and have found the shortest way through the curtain to make their first orientation flight. They fly off, participate in massed flight and land at the 'mouth' zone on the sunny side of the nest after 2–5 min. We do not know, however, whether they crawl back to their original places below the curtain again, or are pushed into new tasks at other nest sites.

Second, bees from the surface layer of the curtain are motivated for the participation of massed flight possibly by the sudden active environment. These bees are also young bees, 'callows' with pale yellow abdomen. According to Otis et al (1990) they subsequently move to outer curtain positions during their first part of life. They protect the nest by holding off heat, rain and wind, and participate in food storage and defense (Roepke, 1930; Michener, 1974; Ruttner, 1988; Seeley, 1995). We found that nearly half of these roofing bees had changed their position during massed flight activity, which means that this outer layer of the curtain is reorganised periodically at least twice a day.

A special kind of massed flight activity in *A dorsata* occurs immediately after sunset and has already been described as drone flight (Koeniger and Wijayagunasekera, 1976; Koeniger et al, 1988; Koeniger et al, 1994). We observed that this kind of massed flight affected only a small part of the colony.

ACKNOWLEDGMENTS

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Zusammenfassung — Verhaltensbeobachtungen während periodischer Massenflug-Aktivität bei der Indischen Riesenhonigbiene *Apis dorsata.* In Delhi, Assam und Nepal konnte eine periodische Form von Massenflug-Aktivität bei *Apis dorsata* Fabricius, 1798 beobachtet und anhand von Video-Aufzeichnungen (Abb 1) und Bildanalyse-Technik untersucht werden. Zwei bis fünf mal am Tag tritt das Nest vom normalen, ungestörten Zustand scheinbar spontan für nicht mehr als 5 Minuten in einen Zustand höchster Erregung (Abb 2). Dieses tagtäglich wiederkehrende Verhalten wurde über mindestens 2 Monate an einem Nest in Delhi beobachtet. Während solcher Massenflug-Aktivität ändert sich die Struktur der Wabenbedeckung, des sogenannten Bienenvorhangs, in sehr auffälliger Weise. Die in der äußersten Schicht hängenden Vorhangbienen verlassen dann den Ort, an dem sie vorher stundenlang bewegungslos verharrten, beginnen umherzulaufen und fliegen schließlich weg. Die Körperausrichtungen und die Position dieser Bienen verändern sich (Abb 3), dabei entsteht aus dem bei Ruhe geordneten Muster parallel hängender Bienen innerhalb kurzer Zeit ein scheinbares Durcheinander sich nach allen Richtungen bewegender Bienen (Abb 2,3). In dem einen Nest in Delhi, das wir im Detail untersuchten, flogen rund 20% der Nestbienen im Laufe von 5 min ab, dabei waren zu jedem Zeitpunkt während der gesteigerten Flugaktivität maximal 2-3% der Kolonie vor dem Nest in der Luft. Ein signifikanter Anteil von Bienen (Abb 4), der von der beschatteten Seite des Nestes abgeflogen war, landete auf der Sonnenseite im Bereich der aktiven Zone, des sogenannten 'Nestmundes'. Der mittlere Bewegungsindex der Vorhangbienen der äußeren Schicht war in den Ruhephasen unter 0.3 mm/s und stieg in den Aktivitätsphasen auf 1.0 mm/s (Abb 5). Es gibt wohl mehrere verschiedene Ausprägungen von Massenflug-Aktivität bei *A dorsata*, die mit Verteidigungsverhalten, Migration, Schwärmen und dem Drohnenflug zusammenhängen. Jene Form von Massenflug-Aktivität, wie wir sie beobachten konnten, unterscheidet sich von den Defäkationsflügen (die im Zusammenhang mit dem sogenannten 'Gelben Regen' beschrieben wurden) dadurch, daß sie nicht durch Temperatur als kritischen ökologischen Faktor ausgelöst ist. Diese Form der Massenflugaktivität bewirkt, daß Jungbienen aus unteren Schichten im gesamten Vorhangsbereich durch diesen nach außen stoßen und dort ihren Orientierungsflug durchführen. Während jeder 5-minütigen Massenflug-Aktivität tauscht sich die äußerste Schicht (nicht aber die Schicht darunter) auch auf der ruhigen beschatteten Seite zu mehr als 50% aus. Dies führt periodisch, pro Tag mindestens zweimal, zu einem partiellen 'Schichtwechsel', wobei die darunterliegende Schicht nach und nach zur Außenschicht wird. Auf einem *Ficus*-Baum in Assam mit mehr als 100 Nestern konnten wir 15 Massenaktivitäten mitverfolgen (Abb 6). Es ist anzunehmen, daß zu einem bestimmten Zeitpunkt meist nur eine Kolonie daran beteiligt war.

***Apis dorsata* / Massenflug-Aktivität / Orientierungsflug / Bildanalyse / Indien**

Résumé — Caractéristiques comportementales d'une activité de vol en masse chez l'abeille géante, *Apis dorsata.* À Delhi, en Assam et au Népal, une forme périodique d'activité de vol en masse chez *A dorsata* Fabricius, 1798 a été observée et étudiée par enregistrement vidéo (fig 1) et analyse d'images. De deux à cinq fois par jour le nid passe spontanément, semble-t-il, d'un état normal non perturbé à un état d'agitation élevée qui dure environ 5 minutes (fig 2). Ce comportement, qui se reproduit chaque jour, a été observé sur un nid à Delhi pendant au moins 2 mois. Durant cette activité de vol en masse la structure de la couverture des rayons, nommée rideau d'abeilles, se modifie de façon spectaculaire. Les abeilles de la couche extérieure quittent l'endroit où elles étaient restées immobiles des heures durant, se mettent à courir çà et là et finalement s'envolent. La direction des corps et la position de ces abeilles se modifient (fig 3). En période de repos les abeilles, toutes parallèles en position verticale, forment un motif bien ordonné ; en peu de temps il se transforme en un imbroglio apparent d'abeilles s'agitant en tous sens (figs 2 et 3). Dans un nid étudié en détail, près de 20 % des abeilles se sont envolées en l'espace de 5 minutes et le nombre maximal d'abeilles en vol stationnaire devant la ruche représentait 2 à 3 % de la colonie pendant la période d'intense activité de vol. Un pourcentage significatif d'abeilles (fig 4), qui avait quitté le côté ombragé du nid, se posait sur le côté ensoleillé dans la région de la zone active, appelée «bouche du nid». L'index moyen d'agitation des abeilles de la couche externe était de 0,3 mm/seconde durant les phases de repos et montait à 1,0 mm/seconde dans les phases d'activité (fig 5). Il existe bien d'autres expressions de l'activité de vol en masse chez *A dorsata* qui sont liées au comportement de défense, à la migration, à l'essaimage et au vol des mâles. Chaque forme d'activité de vol en masse se distingue des vols de propreté (liés à ce qui a été décrit sous le nom de «pluie jaune») par le fait que la température n'est pas le seul facteur écologique déclenchant. Cette forme d'activité de vol en masse a pour conséquence que les abeilles jeunes de la couche inférieure arrivent à la surface du rideau d'abeilles et exécutent leur premier vol d'orientation. Durant chaque période de 5 minutes de l'activité de vol en masse, plus de la moitié de la couche externe (mais pas la couche interne) se renouvelle sur le côté ombragé et calme du nid. Ceci conduit périodiquement, au moins deux fois par jour, à un mélange partiel des couches, au cours duquel la couche du dessous devient progressivement celle du dessus. Sur un *Ficus* en Assam, qui hébergeait plus de 100 nids, nous avons suivi 15 activités de vol en

masse ; la plupart du temps, à un moment donné, une seule colonie était concernée.

***Apis dorsata* / activté vol / comportement social / vol orientation / analyse image / Inde**

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