Six-Year Population Fluctuation of the Giant Honey Bee *Apis dorsata* (Hymenoptera: Apidae) in a Tropical Lowland Dipterocarp Forest in Sarawak

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ABSTRACT   The giant honey bee *Apis dorsata* F. inhabits lowland tropical rainforests in Southeast Asia, where a general, community-wide flowering occurs at intervals of 4 yr on average. The numerical response by the honey bee population to the drastic increase of flower resources during general flowering was investigated for 6 yr by monthly light-trapping and by nest counts in a lowland dipterocarp forest in Borneo. The numbers of *A. dorsata* workers obtained by light-trapping were highest during general flowering periods, whereas very few workers were trapped in other periods. The abundance of *A. dorsata* nests showed temporal correspondence with the abundance of trapped workers, and the nests disappeared in the nonflowering periods. These data suggest that the *A. dorsata* population increases rapidly in response to general flowering and that this is initiated by nonseasonal, long-distance migration. Drones of *A. dorsata* were present during the general flowering period, but there is no evidence that reproduction by *A. dorsata* occurs only in general flowering periods. Fluctuation in abundance by the honey bee *A. koschevnikovi* Enderlein was also observed by monthly light-trapping. The temporal trend of this species was similar to that of *A. dorsata*, but sightings persisted even in the nonflowering periods. Both honey bees responded numerically to floral resources, but long-distance migration in *A. koschevnikovi* was unlikely.

KEY WORDS   *Apis koschevnikovi*, Southeast Asian tropics, Borneo, general flowering, numerical response, migration

HONEY BEES ARE abundant flower visitors of tropical and temperate vegetation (Roubik 1978, 1980; Seeley 1985, 1995). Their capacity to visit large numbers of flowers is generated by a large colony size, highly developed flight ability, and efficient communication with nest-mates while foraging. Furthermore, the wide range of flowers available allows honey bees to select flowers that are most profitable in their energy budget at a given time and concentrate their foraging efforts on them (Frish 1967; Seeley 1985, 1995; Roubik 1989; Dyer and Seeley 1991b). Colonies may change the target flowers as flowering phenology proceeds (Seeley 1985, 1995).

The giant honey bee *Apis dorsata* F. of tropical Asia (Seeley 1985, Ruttner 1988) has the largest natural colony size among all the honey bee species (Dyer and Seeley 1991a). Because this species may affect the pollination system and reproduction of many angiosperm species, it is important to elucidate its biology for understanding the ecological processes and mechanisms that maintain the very diversified pollination systems in the tropical rain forests. In fact, it was suggested by Momose et al. (1998) that *A. dorsata* is a major pollinator of several dominant components of forest canopy in Southeast Asian lowland dipterocarp forests, which is one of the richest terrestrial ecosystems in the world.

The vegetation of the wettest lowland of Southeast Asia is characterized by dipterocarp trees with a height of >60 m and "general flowering." Most tree species of the canopy mass-flower within several months, during which tree species are flowering sequentially, but only every 4–5 yr (Yap and Chan 1990, Ashton 1991, Appanah 1993, Sakai et al. 1999). Momose et al. (1998b) reported that *A. dorsata* was one of the major flower visitors in the general flowering event of 1992 in a lowland dipterocarp forest in Borneo. Because many large-sized canopy tree species produce a large number of flowers and consequently yield a large amount of nectar and pollen in a general flowering event (Momose et al. 1998b), they would provide *A. dorsata* with abundant food. However, the supply of nectar and pollen drastically decreases when general flowering events end. The intervals of general

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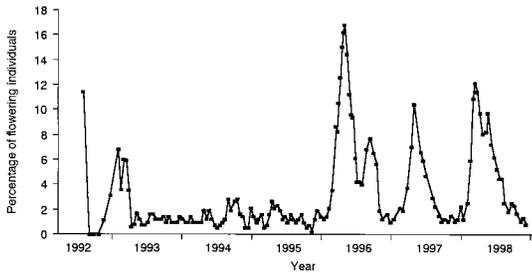
Fig. 1. Changes in flowering intensity at Lambir Hills National Park, Sarawak, Malaysia (illustrated after Kato et al. (2000) with our updated data). Flowering intensity is represented by flowering percentage of ≈420 individuals representing ≈300 species.

Fig. 2. Nests of *A. dorsata* on the study tree, *Koompasia excelsa* (taken on 28 February 1998). Arrows indicate nests.

flowerings are irregular and probably longer than the period that honey bee colonies can survive without abundant floral resources. How do they survive the nongeneral flowering periods? Do they switch the target flower species, or switch their foraging habitat? This issue affects not only life history strategy and population dynamics of *A. dorsata* but also the reproductive biology of many tree species. Although long-term population fluctuation of another *Apis* species and some 60 bees have been studied in the Americas (Wolda and Roubik 1986, Boreham and Roubik 1987, Roubik and Boreham 1990, Roubik 2000, Roubik and Wolda 2001), similar information is not available for *Apis* or any other bee species in the Asian tropics.

A few studies have reported that *A. dorsata* performs long-distance migration (Koeniger and Koeniger 1980, Dyer and Seeley 1994). However, the reported cases of migration by *A. dorsata* were seasonal, and it is not known whether *A. dorsata* colonies migrate in response to a community-wide general flowering at irregular intervals.

In this study, we monitored the numerical response of *A. dorsata* in relation to general flowering by examining changes in the abundance of *A. dorsata* over 6-yr period through monthly light-trapping and a 3-yr period through monthly censuses of nesting colonies. Moreover, we attempted to detect reproduction in *A. dorsata* by recording catches of drones of *A. dorsata* in the light traps. Because workers and drones of another honey bee species, *A. koschevnikovi* Enderlein, were also caught in the light traps, the numerical response and reproductive seasons of the species were also analyzed.

Materials and Methods

Field work was conducted in the lowland dipterocarp forest of Lambir Hills National Park, Sarawak, Malaysia. Details of the study site were described in Inoue and Hamid (1994, 1997) and Inoue et al. (1995). General flowering occurred at the study site between March and August 1992, March and November 1996, March and June 1997, and February and July 1998 (Momose et al. 1998b, Sakai et al. 1999, Kato et al. 2000; Fig. 1). The pollination syndrome and reproductive

ecology of some tree species that displayed general flowering have been studied in and around the 8-ha plot, which is the core sight of the study site, by Momose et al. (1998a, b).

Momose et al. (1998b) revealed that at least 15 species of emergent and canopy trees, mainly belonging to Dipterocarpaceae, were visited and pollinated by the giant honey bee *Apis dorsata. A. dorsata* workers visited flowers from dawn until dusk, even in twilight, and sometimes at night (Dyer and Seeley 1991a). They were caught by light-trapping and often observed visiting nocturnally opening flowers (Oldroyd et al. 1992, Momose et al. 1998b). *A. dorsata* is known to construct nests in open spaces, such as on rock walls of cliffs, and branches of tall trees, to avoid predation (Seeley 1985). Nests are often observed to be built on the under-side of big branches of emergent trees (Fig. 2). The honey bee *A. koschevnikovi* is also one of the major pollinators in general flowering at the study site (Momose et al. 1998b). This species constructs its nest in tree hollows. Nests of this species were observed in artificial wooden hives put on canopy towers.

The details of the light trap and the procedure were described in Kato et al. (1995). To monitor fluctuations in population size of *A. dorsata* and *A. koschevnikovi*, monthly light-trapping was conducted from August 1992 to August. 1997 and from April 1998 to November 1998 using modified Pennsylvania UV light-traps consisting of a 20-W mercury vapor lamp, two crossed transparent boards for intercepting light-attracted flying insects and a bucket to capture the fallen insects. Three light traps were set up at a fixed site, 1, 17, and 35 m above the ground of a tree tower. The light-trapping was conducted in four consecutive days during a new moon when there is the least celestial light. Because *A. dorsata* drones fly at dusk (Rinderer et al. 1993, Tan et al. 1999), they can also be caught by light-trapping. Workers (or drones) caught during each period (of four consecutive days) were grouped and constituted a monthly catch.

In addition to light-trapping, the number of *A. dorsata* nests made on branches of a selected emergent tree, *Koompasia excelsa* (Becc.) Taubert (Leguminoseae), at the study site was censused monthly from December 1996 to December 1999. The tree was
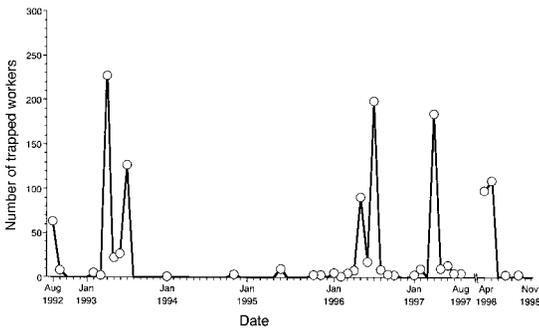
Fig. 3. Temporal trend in monthly light-trap catches of *Apis dorsata* workers from August 1992 to December 1998. A circle indicates the monthly catch by light-trapping (four consecutive days around the new moon), when at least one individual was trapped. For the months when no worker was trapped for the four consecutive days, no circle is given and the line indicates zero.

located ≈900 m away from the site of light-trapping. This species is a typical emergent tree and appears to be a preferred nest site of the *A. dorsata.* In every census, we used binoculars to determine whether honey bee individuals were present on nests. If no honey bee individuals were detected on a nest, we omitted the nest from the count. Throughout the study period, censuses of tree flowering and fruiting phenology (Sakai et al. 1999) revealed that only two other nest sites of *A. dorsata* were found in or near the 8-ha plot (T.It and T.N., unpublished data). Nests at the two sites were difficult to count and monitor due to multiple canopy layers and shortage of manpower, and these nest trees were much less preferred, compared with the study tree.

Results

Monthly light-trap catches of *A. dorsata* workers increased drastically in February–July 1993 with a peak in April (February–July in 1993), March–August 1996 with a peak in July (March–August in 1996), and in April–June 1997 with a peak in April (April–June in 1997) (Fig. 3). Worker catches were also relatively high in August 1992 (August in 1992) and in April–May 1998 (April–May in 1998) (no data were available previous to these two periods). Most of the other monthly catches yielded zero or at most only several workers. Of the five periods of abundant *A. dorsata* workers, only the February–July in 1993 did not coincide with a general flowering event. Drones were found only in four consecutive monthly catches, April–July 1996, coincident with the workers' increase during a general flowering period.

The number of active nests of *A. dorsata* ranged from 4 to 8 from December 1996 to September 1997 (Fig. 4). Thereafter, all active nests disappeared, and none was found until January 1998. The number of nests increased drastically between February and March 1998 and remained high until May 1998. Between May and June 1998, active nests drastically
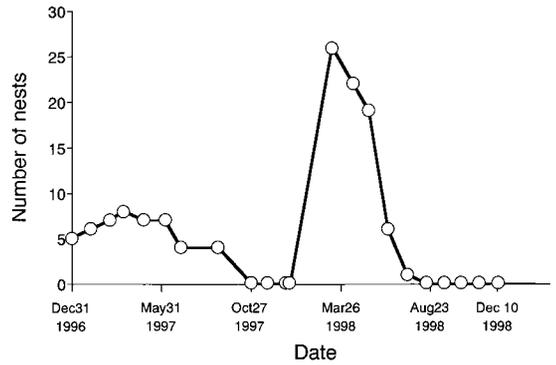
decreased and disappeared at the end of August. Since then, no nests have been found at the study tree.

Workers of *A. koschevnikovi* were caught frequently after August 1995, with the number of workers showing several peaks (Fig. 5). Before that time, workers were found only in several monthly catches, and the numbers of workers did not exceed 10 except in July 1993. Drones of *A. koschevnikovi* were found only in 2 mo, April and May 1996.

Discussion

The correlation between the number of trapped *A. dorsata* workers and the number of nests suggests that the number of *A. dorsata* workers caught by light-traps is a good indicator of the population levels. The yearly change in the number of nests at another nest site in the study area from August 1992 to November 1996 (censuses were done once a year on average) also correlated with the change in light-trap catches and flowering events, although these nests sites were much less preferred (the maximum number of nests were seven), compared with the study tree (Nagamitsu 1998). Moreover, few *A. dorsata* workers were collected during nongeneral flowering periods (K.M.,
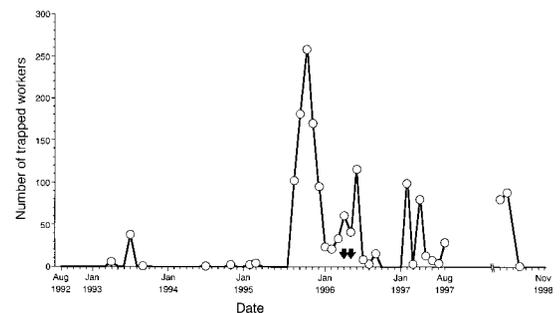

Fig. 4. Temporal trend in the number of active nests of *Apis dorsata* on the study tree from December 1996 to December 1998.

Fig. 5. Temporal trend in monthly light-trap catches of *Apis koschevnikovi* workers from August 1992 to December 1998. An arrow indicates the monthly catch including one trapped drone. For other symbols, see Fig. 3.

unpublished data) in flowering-phenology censuses, which were conducted twice a month throughout the study period at the study site (see Momose et al. 1998b and Sakai et al. 1999 for the details). All these lines of evidence suggest that light-trap catches reflect abundance and swarming activity of both highly eusocial honey bees and stingless bees, and honey bee abundance in light traps correlates well with regional swarm and nest abundance (Wolda and Roubik 1986, Roubik 2000, Roubik and Wolda 2001).

Population fluctuation of *Apis mellifera* L. has been studied in Panama for 10 yr by the same light-trapping method (Wolda and Roubik 1986, Boreham and Roubik 1987, Roubik and Boreham 1990, Roubik 2000, Roubik and Wolda 2001). These studies revealed that honey bee abundance peaks about 1 mo after peak flowering periods during mid dry season and early wet season in the lowland moist forest. Seasonal abundance peaks are nearly the same from year to year, but a year characterized by an El Ñino southern oscillation may produce a large increase in honey bee abundance a few months after the dry season flowering peak. These patterns in Panama differ from those described for *A. dorsata* in two ways. First, the population fluctuation of *A. dorsata* was more drastic than those in Panama; abundance of *A. dorsata* was extremely low, virtually zero, in nonflowering periods, while it increased rapidly to remarkably high levels in flowering periods. Second, although the population increases corresponded to the increases in flower abundance in *A. dorsata*, they were not annual. These two discrepancies may be associated with the difference in climate between the two areas: the alternation of dry and wet seasons is more distinctive in Panama than that at our study site. In addition, the phenomenon of general flowering is absent in Panama.

The results, along with some circumstantial evidence, indicate that the numerical response of the *A. dorsata* population is generated by immigration. The following four reasons support the argument that *A. dorsata* was largely absent in nonflowering periods and immigrated from outside areas at the beginning of general flowering. First, the number of trapped workers and nests remained virtually zero in nonflowering periods. Second, diurnal censuses of floral visitors yielded very few *A. dorsata* workers (K.M., unpublished data). Third, because the increase in the number of nests was quite large, it is unlikely that this increase was generated by colony reproduction through swarming. Fourth, because the forest was surrounded by disturbed areas such as secondary forest with heath, oil palm plantation, slash-and-burn fields and their abandoned grasslands, it is unlikely that there were sufficient food resources to maintain *A. dorsata* colonies in neighboring areas of the study site.

Apis dorsata populations are known to migrate distances of 50–100 km (Koeniger and Koeniger 1980, Dyer and Seeley 1994). These two instances were suggested to be seasonal responses to predictable annual alternation of dry and wet seasons and associated changes in flower abundance. However, at our study site, the annual or seasonal climatic change was very weak, and the flower abundance fluctuated not annually but irregularly and supraannually. Thus, it is suggested that *A. dorsata* colonies in tropical lowland rainforests, adopting long-distance migration, are able to collect large amounts of food that is available during irregularly (not annually) occurring general flowering. If *A. dorsata* colonies are restricted to primary forests, the nearest habitable environment was over 50 km from our study site.

How do *A. dorsata* colonies recognize and respond to the occurrence of general flowering, if they migrate long distances? There are at least two possible hypotheses. First, colonies respond to the information provided by scout workers that usually search for areas with more abundant flowers than the current foraging areas. This hypothesis implies that workers fly long distances (>50 km) from their nest sites. Studies on the foraging behavior of *A. mellifera*, where colony size and worker body size are smaller than *A. dorsata*, support the possibility of large foraging areas (Visscher and Seeley 1982, Seeley 1995). Second, colonies respond to the same climatic stimuli that trigger the general flowering. Because the general flowering occurs at regional spatial scale, colonies in different sites, but the same region, may recognize the trigger stimuli and initiate migration. These hypotheses should be examined by more extensive studies on the spatial range and foraging activities of workers and the whole life cycle (growth, reproductive schedule and migration schedule) of individual colonies and the relative flower availability in a region.

The temporal trend in the catches of *A. koschevnikovi* was similar to that of *A. dorsata* (Fig. 5). However, the following three facts suggest that this species may not migrate long distances in response to flower abundance. First, the highest peak of worker catches occurred from October to November 1995 before the next general flowering. Second, *A. koschevnikovi* was absent in the general flowering period in late 1992. Third, an active nest of this species has been present for at least 3 yr (first found in May 1996) near the light-trapping site. The colonies never relocated during this period, even after the cessation of general flowering (T.It and T.N., unpublished data). *A. koschevnikovi* colonies may be able to survive even in nongeneral flowering periods, because the food demands of their small-sized colonies are less than those of *A. dorsata*.

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