

Surfing the Sweet Wave: Migrating Giant Honey Bees (Hymenoptera: Apidae: *Apis dorsata*) Display Spatial and Temporal Fidelity to Annual Stopover Site in Thailand

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Subject Editor: Michael Simone-Finstrom

Received 4 March 2021; Editorial decision 28 April 2021

Abstract

Apis dorsata F. (Hymenoptera: Apidae), the giant honey bee of southern Asia, is an important pollinator of crops and non-cultivated angiosperms, and a producer of honey and beeswax. Its populations are in decline in many areas. Colonies migrate seasonally between highland and lowland nesting sites, taking advantage of available food sources. In 2009, a stopover site was discovered in Thailand where numerous migrating colonies bivouacked near one another. Bivouacs used the site again in 2010. I went to the site in 2016 to test the hypothesis that bees use the site regularly as part of an annual migration. I witnessed many bivouacs, spanning almost precisely the same time period and occupying the same area as in 2010. Here I describe their migratory dances in preparation for departure and their subsequent flights as well as periodic mass flight and defensive behavior. Analysis of photographs indicated that the bivouacking bees aged slowly and may thus live long enough to be capable of intergenerational transmission of migratory route knowledge. I describe attributes of the stopover site, e.g., abundant food and water availability, its location along a major river, and other possible navigational cues. Although the site is the only one of its kind so far known to researchers, such stopover sites probably exist wherever giant honey bees undertake long seasonal migrations. I recommend searching for bivouacking sites, particularly along rivers, wherever giant honey bees migrate. Stopover sites are undoubtedly essential to the life history and health of migratory bee populations, and thus warrant conservation policies.

Key words: bivouacs, giant honey bee, longevity, migration, stopover

The giant honey bee, *Apis dorsata* F. (Hymenoptera: Apidae), ranges across southern Asia from Pakistan to the Philippines, and from southern China to Indonesia (Ruttner 1988, Hepburn and Radloff 2011). It is a major honey and beeswax producer (Oldroyd and Wongsiri 2006) and pollinator of both agricultural crops and non-cultivated angiosperms throughout its range (Corlett 2011, Partap 2011, Sihag 2014). There is evidence that its populations are dwindling, and extensive extirpation is a threat due to overharvest of honey, destruction of forest habitat across southern Asia (Laurance 2007), and felling of tall trees that colonies use as nest sites (Oldroyd and Wongsiri 2006, Oldroyd and Nanork 2009, Corlett 2011, Sihag 2014).

Entire colonies of *A. dorsata* migrate regularly, with changes in the monsoon season, back and forth between highland and lowland nesting sites. While nesting, a colony typically builds a single, exposed, 1–1.5 m-wide wax comb on which its population may grow to >50,000 individuals (Morse and Laigo 1969) before reproducing by swarming (colony fission). Dozens—even hundreds—of nesting colonies may aggregate at close quarters in a single tall tree or other

lofty structure, such as a water tower (Oldroyd et al. 2000, Oldroyd and Wongsiri 2006, Hawkeswood et al. 2019).

Colonies typically migrate to take advantage of changing bloom, at different altitudes, of flowering plants that provide their diet of nectar and pollen. In northern Thailand, at least, this appears to involve moving to higher elevations to increase colony population and reproduce by swarming with the onset of the dry season, then returning to lower elevations to build another nest, grow, and swarm again in the wet season (Thapa et al. 1998, Oldroyd et al. 2000, Oldroyd and Wongsiri 2006, Robinson 2012). However, details of seasonal movement vary across Asia (Koeniger and Koeniger 1980, Dyer and Seeley 1994, Sihag 2014). Some populations, including those in the Philippines, reportedly do not migrate at all (Morse and Laigo 1969). Others apparently migrate nomadically and non-seasonally, opportunistically availing themselves of sporadically available floral bloom (Itioka et al. 2001). Microsatellite DNA techniques have been used to demonstrate that colonies or their offspring colonies may return to the same exact nesting location year after year (Neumann et al. 2000, Paar et al. 2000). The authors of those

homing-fidelity studies expressed surprise at their findings, given limited studies indicating that *A. dorsata* workers have life spans of only a few weeks (Otis et al. 1990, Chinh et al. 2004)—much shorter than the approximately 6 mo that would be required for them to have first-hand knowledge of a former nest site. Speculation and some experimentation as to how colonies might return to such sites has ensued (Oldroyd and Wongsiri 2006, Liu et al. 2007, Hepburn 2011). Among other hypotheses, Oldroyd and Wongsiri (2006) speculated that if some worker bees live ~6 mo or more, thus constituting a potential ‘memory guild,’ these older bees might be able to recall a former nesting site and guide their colony back to it along a previously used, memorized route.

Migration routes have only been inferred by researchers. Colonies abandon combs at a well-known nest site; bees then appear, sometimes weeks later, and build new combs at another established nest site up to 200 km away (Koeniger and Koeniger 1980). No one has managed to track migrating giant honey bees over long distances. Bivouacking bees, which pause during migration and form hanging clusters without building comb, have only rarely been seen by researchers. Koeniger and Koeniger (1980) reported scattered bivouacs in Sri Lanka, where migrating bees may take as long as a month to reach their destination. Underwood (1989) observed widely dispersed wintering bivouacs of the closely related Himalayan montane species *Apis laboriosa* in Nepal. In contrast to those reports, Robinson (2012) described a thus-far-unique ‘bivouac congregation stopover site’ (BCSS) at a mango (*Mangifera indica* L.; Sapindales: Anacardiaceae) orchard near Mae Hong Son in northern Thailand, where large numbers of bivouacs gathered over a period of ~2 mo, in the autumns of both 2009 and 2010.

Animals of many taxa that engage in strenuous long-distance migrations pause at predictable stopover sites to rest and replenish energy reserves. Such sites have been extensively studied in birds, where a wide variety of species demonstrates annual fidelity to the sites (Moore et al. 1995, Newton 2010). Migrating herbivorous waterfowl, for example, take advantage of the phenology of spring greening of plants at staging sites, a phenomenon van der Graaf et al. (2006) called ‘green wave surfing.’ Research using geolocators on North American ungulate mammals indicates that favored stopover sites that contain prime vegetation along their route are vital to the migrating animals. They ‘surf’ the green wave, feeding as they move in conjunction with the availability of nutritious plants (Merkle et al. 2016). Some ungulate migration routes are culturally transmitted, passed by learning from generation to generation (Jesmer et al. 2018).

For the current study, I visited the *A. dorsata* BCSS in 2016, 6 yr after Robinson’s (2012) field investigations, to test the hypothesis that giant honey bees would continue to use the same location at the same time of year, thus providing evidence that the site is an integral part of a predictable, seasonal migration (Hepburn 2011, Dingle 2014, Rubenstein and Alcock 2018). I studied migration dances the bees performed in preparation for departure from the site, then tracked the initial directions of their subsequent flights. I also conducted photographic observations to test the hypothesis that bivouacking worker bees age more slowly than nesting bees, thus potentially living long enough to recall prior nest sites.

Materials and Methods

Ethics Statement

Permission for access to the Mae Hong Son Agricultural Research and Development Center was granted by its director, Mr. Natthanon

Fusang. No permits were required for the limited insect collecting required to gather voucher specimens. The study did not involve endangered or protected species. I made every effort to avoid interfering with the bees’ normal migratory behavior.

Study Site

The study site was the area that Robinson (2012) termed a BCSS. It is a long, narrow mango orchard stretched along the Pai River. The orchard and its immediate surroundings are associated with the Mae Hong Son Agricultural Research and Development Center, elevation 200 m, 19.267 N, 97.944 E. The center is surrounded by steep hills covered in deciduous, largely teak (*Tectona grandis*) forest. I revised Robinson’s (2012) schematic map to reflect a bend in the river and in the transect road used for searching for bivouacs (Fig. 1). The revision also records the replacement in 2016 of a block of passion fruit that bordered the mango orchard in 2010 with vegetable crops (along the river, northeast of the riverside mango orchard). While the rainy season in 2009 was abnormally dry and that in 2010 was abnormally wet (Robinson 2012), cumulative precipitation from July through November 2016 was 742 mm, 22% below average (data from Mae Hong Son Airport weather station).

Bivouac Survey Methods and Measurements

I followed the methods Robinson (2012) described, with minor variations. Beginning 24 August, I conducted twice-daily surveys, in early morning and mid-afternoon, by bicycling slowly for ~2.5 km along the road to the west of the riverside mango orchard (Fig. 1) in search of bivouacs. I looked carefully on both sides of the road along the orchard and extended the search ~1 km both north and south of the area mapped in Fig. 1. Every 2 d, I searched the other mango orchard shown on the map, west >100 m from the river, but never observed bees there. I also regularly traveled through northern Thailand both near the study area and well outside it, constantly looking for bivouacs without success. This included, for example, a daily bicycle ride of ~10 km to and from the village of Mae Hong Son, through human settlements, agricultural and forested land. I also sometimes patrolled the study site during lulls in activity of the colonies I was studying. I occasionally found new bivouacs as I made rounds studying those already present.

I discovered the first bivouac on 18 September, resting in a mango tree in the orchard (Fig. 2). Another swarm arrived the following day. Bees then arrived and departed steadily through 18 November, when the last bivouac departed the study site. I continued to ride bicycle transects and search the study site daily through 30 November, to bracket the dates of Robinson’s (2012) studies and ascertain that no more bees were arriving. By the end of November, flowering had ceased in the nearby *Eucalyptus* and teak trees. Deciduous trees in the area were shedding their leaves with the onset of the dry season.

Bivouacs were distinguishable by their widely varying sizes and shapes. Upon finding a new bivouac, I attached an identifying tag to a nearby branch. Except for 3 that took short flights that I was able to track, bivouacs did not move around the study site before leaving it completely, so there was no potential for confusing one with another.

I recorded arrival time as the date I first saw the bivouac. Often this was very precise, as I saw many swarms arrive and land. In rare cases, the recorded date could be late by as much as several days, if a newly arrived swarm went unnoticed. I recorded departure time as the date at which I first noted the bivouac’s absence. Again, in many cases, I saw swarms depart the study site; in other instances, the swarm may have left the previous afternoon, but its absence was not noticed until

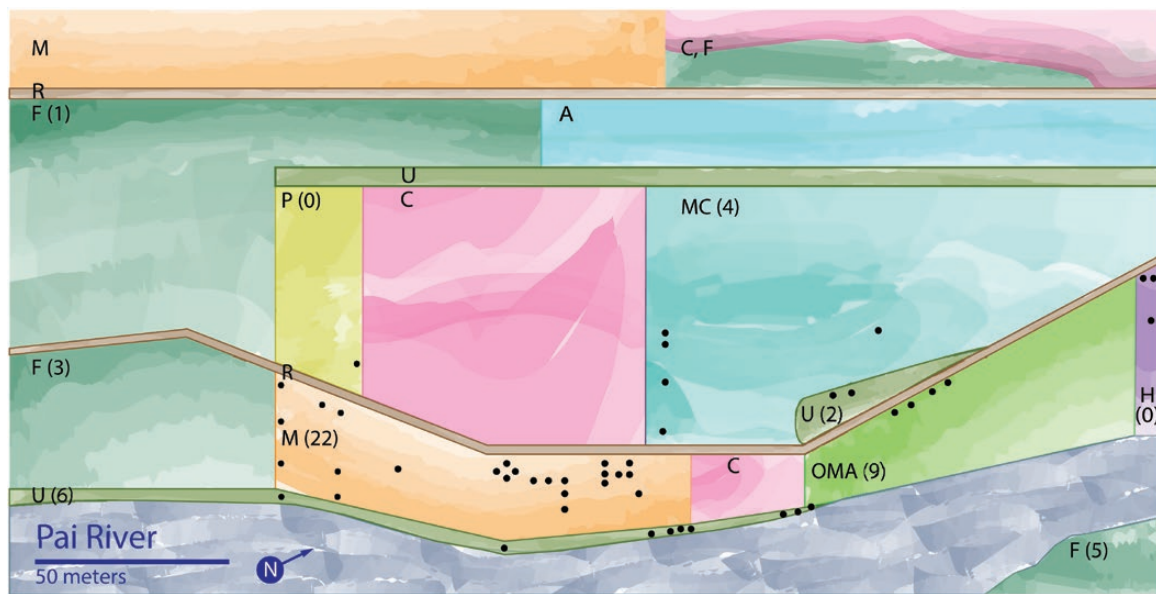


Fig. 1. Study site map to scale showing locations of bivoacs (black dots). Note concentration of bivoacs in riverside mango trees, and lack of them in mango trees >100 m from the river. In parentheses for comparison are the combined numbers of bivoacs [Robinson \(2012\)](#) recorded in each vegetation block in 2009 and 2010. One other bivoac was seen ~1 km NE of the depicted study site, along the transect road. A = airstrip; C = vegetable crops; F = forest; H = housing and offices with trees; M = mango orchard; Ma = macadamia orchard; OMA = old mango trees; P = pomelo orchard; R = transect road; U = undergrowth.



Fig. 2. A large bivoac rests on the underside of a mango limb at the study site.

morning. In calculating the mean length of stay, I recorded a stay as 0.5 d if it departed the same day it arrived, 1 d if its absence was noticed the day after arrival, 2 d if it was gone 2 d after its arrival, etc.

I used a tape measure to measure colony size and height at which swarms rested. For occasional lofty colonies, I estimated height by sighting against a 3-m reference pole, and colony dimensions using the known 17-mm length of an *A. dorsata* worker as a reference. Because I could not always see all sides of distant or inaccessible colonies, I did not attempt to estimate swarm volume. Rather, I recorded maximum length and width of the colonies. I present these measurements as approximate surface area of one side of the bivoac. Their depth was approximately the diameter of the branch on which they rested, normally ~10–20 cm.

Angles of branches on which the swarms rested were measured in degrees of departure above the horizontal to the nearest 5°, using an 18-inch True Angle Tool (CompoundMiter.com, San Ramon, CA).

I patrolled the bivoacs on a 30–60 min circuit, observing any dancing worker bees, and apparent preparations for swarm flight. Bivoacs were often low in the trees and easily viewed from 1 to 3 m with the unaided eye. I used Leupold 10 × 42 binoculars to view higher swarms. I photographed and video-recorded the bees' behavior using a Canon Power Shot SX10 IS digital camera.

Migration Dances and Flights

In the field, I measured duration of waggle dance circuits ([von Frisch 1967](#)) to the nearest second with a digital stopwatch. For bees dancing repeated circuits a mean time was calculated, again to the nearest second, though individual bees were remarkably consistent in their dances. Note that for longer dances circuit integrity breaks down ([Fig. 3](#)); a dancing bee performs a waggle run, but instead of returning to the site where the run began, the dancer turns and does another waggle run, or moves to another site on the mantle and does its waggle run or a series of runs ([Koeniger and Koeniger 1980](#), [Dyer and Seeley 1991](#), [Robinson 2012](#)). For dances lasting ≥ 3 s, I therefore measured duration just of waggle runs, not entire circuits. I measured the angle of waggle runs to the nearest 15°, using the True Angle Tool.

When a swarm flew, I used a compass to determine its flight direction to the nearest 5° by sighting a line from point of takeoff to point of disappearance or observed landing. I used the [NOAA Sun Calculator \(2016\)](#) to find the sun's azimuth at flight time. To test the hypothesis that dance direction and duration were correlated with flight direction and distance, I then compared the direction and, when possible, distance of the flight to that indicated by the dances.

For presentation in this paper, I converted directions of observed dances to their indicated directions of flight, by adding the measured angle of the waggle run to the sun's azimuth at the time ([Dyer and Seeley 1991](#), [NOAA Sun Calculator 2016](#)).

Worker Longevity

I photographed bivoac number P26 periodically from the same angle during its 42-d stay. Photographs were printed and analyzed

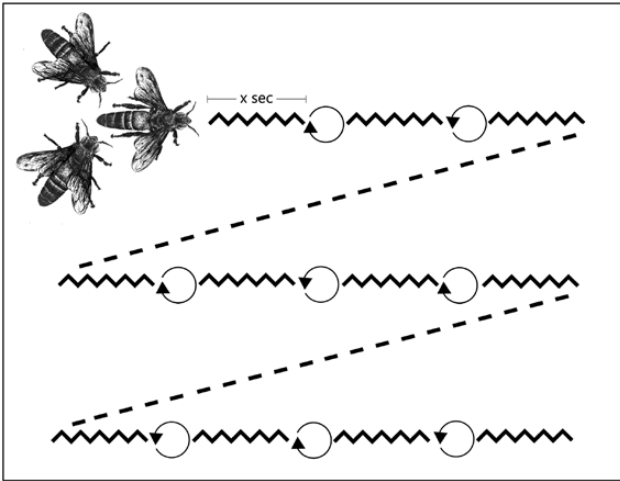


Fig. 3. Diagram of a characteristic long migration dance performed by a worker signaling to followers an imminent departure and relatively long flight. The dancer performs a long waggle run (x -second duration) at a certain angle, circles tightly in one direction, waggles at the same angle for the same duration as in the previous run, circles in the opposite direction, then waggles for the same duration, etc. She then moves to another place on the curtain and repeats the sequence.

to determine the proportion of bees that were ‘callow,’ or young. I determined callowness by judging the relative darkening, caused by black hairs, on metasomal tergites 3–5 (T3, T4, T5) (Michener 2007). My method requires some background, as follows:

Otis et al. (1990) reported in preliminary studies in Malaysia that young *A. dorsata* workers have pale yellow abdomens but develop orange and black abdomens by the time they become foragers. Among the northern Thailand bees of this study, I observed similar color changes. Youngest callows, which mostly hang inactive on the curtain, or in hot weather may ventilate head-downward (Fig. 4), are golden yellow on metasomal tergites 1–5, while T6—the tip of the metasoma, or pygidial plate—is white. (Note that the term metasoma as used here means the abdomen excluding the propodeum, which is fused to the thorax.) As workers age and adopt other duties, the yellow changes gradually to orange, until T1 and T2 of the oldest, dancing scout bees have a dark orange base color. Those performing migration dances always have very dark orange as the T1 and T2 base color. As bees begin active colony defense and foraging, wide bands of hair gradually darken on T5, T4, and T3, in that order. Dancing scout bees have the blackest bands on those tergites. T1 and T2 do not develop black bands. Hair on T6, the pygidial plate, usually turns black, but sometimes remains light-colored even in apparently older bees. Figure 5 shows older bees surrounding a dancing scout in advance of an impending migration, plus mostly older curtain bees.

I designated a worker whose T5 was still either golden or slightly darkening as a callow if there was little-to-no darkening in T4. I then calculated the proportion of these callow curtain bees among all bees whose entire metasomal dorsum could be seen in photographs of bivouac P26, taken at approximately 10-d intervals, viz. day 0 (arrival day), day 11, day 21, and day 36.

Statistical Analysis and Voucher Specimens

All means are reported \pm standard deviations. Chi-square tests of independence were used to compare the percentage of callow bees on the curtain of bivouac P26 at various intervals. Rayleigh tests for the differences between the angles of migration dances and flights



Fig. 4. A golden-yellow callow worker, surrounded by other callows, ventilates by fanning her wings in characteristic head-down, angled posture.



Fig. 5. An aged worker bee, performing the waggle run of a migration dance, is surrounded by recruits, probably of somewhat younger age. Note the especially deep orange and black markings on the dancer's metasoma.

were employed following Batschelet (1981). Voucher specimens of *A. dorsata* collected during this study are housed in the University of Wyoming Insect Museum, Laramie, WY.

Results

Features of Bivouacs

Forty-nine combless bivouacs of *A. dorsata* were observed in the study site in the 2-mo period from 18 September through 18 November 2016. Dates of arrival and departure are shown in Fig. 6. In addition, a single colony constructed a comb in an old mango tree in the area, absconding after 15 d. The abandoned comb was darkened in the center, revealing an apparent attempt at brood rearing, but no brood remained.

The peak number of bivouacs simultaneously on the study site, 16, occurred on 6 October. Many of these were sufficiently clustered that they could be viewed simultaneously from a single location, even given the masking foliage of orchard trees (Fig. 7).

Bivouacs remained on the site for a mean of 9.2 ± 8.0 d, with a median stay of 7 d. Duration of stays ranged from 105 min to 42 d. Of the

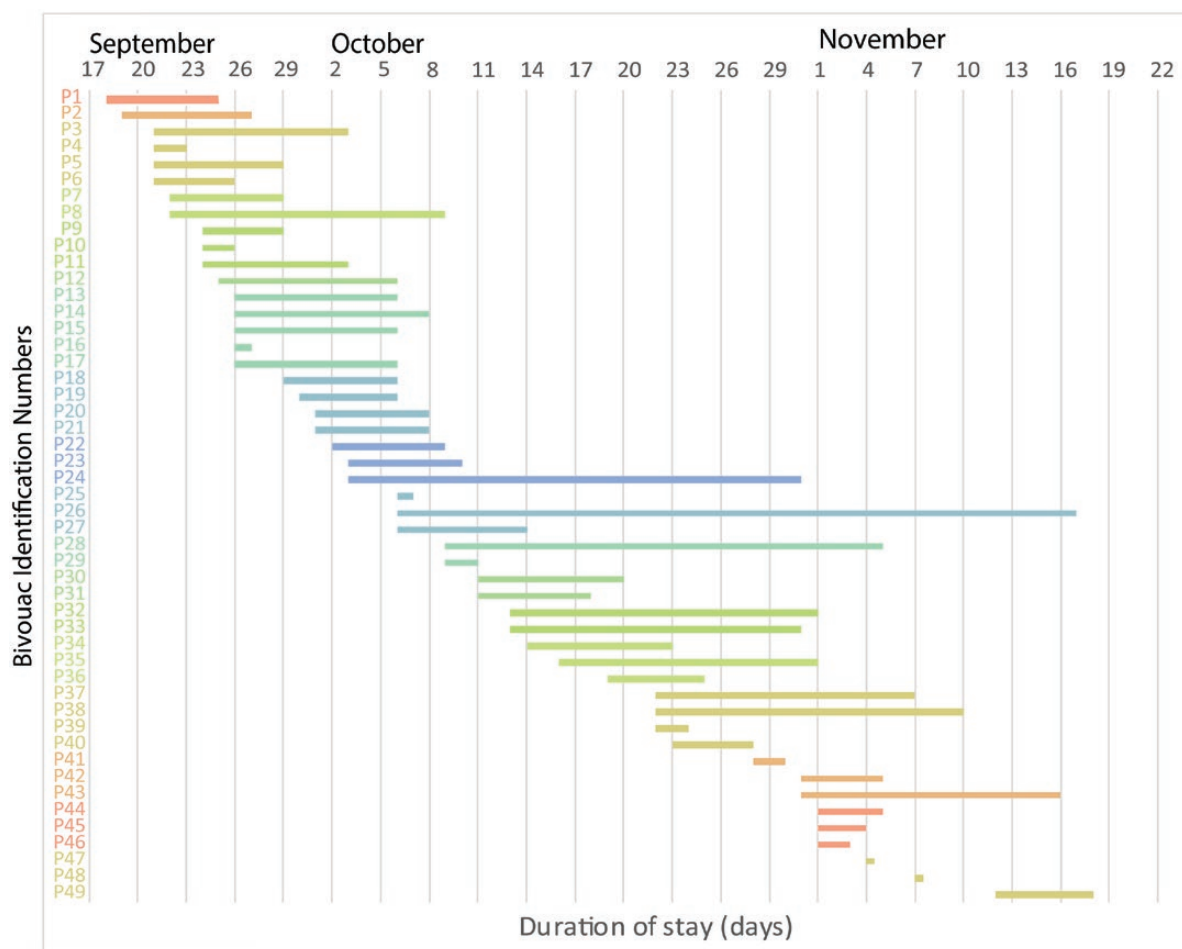


Fig. 6. Timeline chart of bivouac arrival and departure.

49 bivouacs, 24 selected pruned mango trees in the orchard as resting places. Four rested in nearby older, taller, unmanaged mango trees, and eight in unidentified trees of the family Fabaceae between the orchard and the river. Another five were seen in the nearby macadamia (*Macadamia integrifolia*) orchard, two in tall *Delonix regia* trees, and one each in pomelo (*Citrus maxima*) and *Ficus racemosa* trees. Four bivouacs hung in trees of four different unidentified species. Locations of the bivouacs, with comparisons to combined numbers that Robinson (2012) recorded in 2009 and 2010, are plotted on the map in Fig. 1.

Bees perched on branches with a mean angle of $46^\circ \pm 21^\circ$ above the horizontal, with a median of 45° . No bivouacs rested on branches dipping below the horizontal. Mean height at which they rested was 4.9 ± 2.5 m, median 4.5 m. Approximate mean of the one-sided surface area of the bivouacs, rounded to the nearest 10 cm^2 , was $1,790 \pm 2,040 \text{ cm}^2$, median = $1,000 \text{ cm}^2$. Rough estimates of the population size of bivouacs, calculated by counting from photographs all bees on one side and multiplying by the estimated number of columns of bees, ranged from a few hundred to >50,000 bees.

Migration Dances and Flights

All observed bivouac flights from the study site were preceded during the 30 min before departure by a varying number of simultaneously dancing bees. Dancers indicated quite accurately and unanimously ($r = 1$, Rayleigh test; Batschelet 1981), the direction of the impending flights (Supp Table S1 [online only]). For each of nine witnessed flights (Fig. 8), the probability that the direction indicated

by the unanimously dancing bees so closely matched the departure direction by chance alone was extremely low ($P < 0.001$, Rayleigh V-test; Batschelet 1981).

Swarm departures were in widely varying compass directions (Fig. 8; Supp Table S1 [online only]). Accuracy of distance indication of the dances for six of the flights was impossible to gauge, as those swarms disappeared after ~200 m. Duration of the waggle-run portion of the dances for those long flights was consistent among the bees in each bivouac. Among bivouacs it varied from 2 to 6 s. Three short flights of <150 m were preceded by waggle dances with short, 1-s entire circuits (waggle run plus one return to the starting point of the waggle run), indicating the possibility of a correlation between dance duration and flight distance (Fig. 8; Supp Table S1 [online only]). Swarms that took such short flights did not stay long in their new trees. In all three cases these flights occurred in late afternoon and the bees had departed unobserved before my arrival at approximately 0800 h the following morning.

Migration dances occurred away from the 'mouth,' or center of activity at the colony's edge (Morse and Laigo 1969). These dances involved no food sharing, making them readily distinguishable from nectar dances, which almost invariably occurred at the bivouac mouth. Migration dances varied in their structure according to the duration of the waggle run and the apparent flight distances dancing bees were indicating. Dancers were generally closely attended by ~10 workers (Fig. 5). Dances with entire circuits shorter than ~2 s were standard waggle dances in the form described by



Fig. 7. Mango orchard at the BCSS with three visible bivouacs (dark brown) hanging from tree limbs. From left, one bivouac is above the chair, another is at top center of photo, a third, small bivouac is above the bicycle seat. The road in the background was bicycled in surveying for bivouacs.

von Frisch (1967) for *Apis mellifera*. But longer dances, indicating longer flights, took on a different pattern. A dancer performed a stuttering waggle run with the tip of her abdomen raised, made a tight circle to the right or left, then performed another waggle run in the same direction and of the same duration, without returning to the starting point. After that waggle run, she circled in the opposite direction and repeated the waggle, again without returning to the starting point. The series usually continued to the edge of the bivouac. From there the dancer would relocate to another area entirely and repeat the process, maintaining the original waggle-dance angle (Fig. 3). The dancer usually repeated this sequence many times. The repeated waggle portions of the dance thus formed a protracted run whose constant direction accurately indicated flight direction.

Worker Longevity

Over the passage of 5–6 wk, remarkably similar, unchanging proportions (~40–50%) of callow workers were recorded on the outer curtain of a bivouac, P26, selected for photographic analysis (Fig. 9). Chi-squared tests indicated that the proportion of callow bees was statistically the same for all sampled days ($P > 0.1$ for all individual comparisons between days).

Even the 2 d with most differing proportions of callows, day 0 vs. day 11, showed no significant difference ($\chi^2 = 2.61$, $df = 1$, $n = 232$, $P = 0.11$). Those with the most similar proportions, day 0 vs. day 36 and day 11 vs. 21, displayed $\chi^2 = 0.18$, $df = 1$, $n = 219$, $P = 0.67$; and $\chi^2 = 0.22$, $df = 1$, $n = 223$, $P = 0.64$, respectively.

All bivouac volumes, and thus apparent population sizes, remained stable in appearance regardless of how long the bivouacs remained in the study site, indicative that few bees were dying. In addition, I saw no signs of dying bees in and around the bivouacs, except for a few that were lost to predatory hornets *Vespa velutina* and *Vespa tropica*. Though ants were numerous at the study site, especially weaver ants (*Oecophylla smaragdina*), I never saw ants scavenging beneath bivouacs, which one would expect if bees were regularly dying and dropping to the ground.

Other Behaviors

Aside from obvious differences related to comb building and brood rearing, behavior of bivouacking giant honey bees was much like that of those at a nest. A bivouac was curtained by a mixture of young and older workers that were mostly inactive. They hung vertically, head-upward, attached to one another by their legs. Nearly all activity took place at the ‘mouth’ (Morse and Laigo 1969), at the lower edge of one side of the colony, an area from which foragers took off and to which they returned. The size of the mouth was roughly proportional to colony size. Its size increased and decreased with colony activity during the day. Nectar and pollen dancing and forager recruitment took place at the mouth as well. In contrast, relocation or migration dances, when they occurred, were distributed all over the curtain, usually on both sides. Wing-fanning ventilators, mostly light-colored, callow bees (Fig. 4), were common, and numerous in direct sunlight in the heat of the day. While ventilating, many curtain bees ‘gobbed’ (Mardan 1989), exposing fluids on their tongues for evaporative cooling (Fig. 10). When many bees were gobbing, the entire colony sometimes appeared dark and glistening with moisture. Bivouacs also became much more loosely knit at high ambient temperature, increasing air circulation. Foraging and food dancing occurred at rates that varied greatly from bivouac to bivouac; nearly all were for nectar. Pollen dancers appeared rarely on the curtain. They never attracted followers, nor was there any apparent effort by the pollen gatherers to rid themselves of their loads.

Mass defecation flights or ‘periodic mass flights’ (Woyke et al. 2004) occurred regularly throughout the day, once colonies became active at ~22–25°C. Robinson (2012) reported seeing these flights frequently. In 2016, I witnessed 40 of these flights, without ever focusing on them and deliberately studying them. They seemed to happen suddenly, with little apparent preparation aside from a slight agitation and abdominal twitching that spread outward from the mouth through the curtain prior to flight. Flights lasted ~5 min, during which perhaps one-third of the bees flew ~25 m from the bivouac, always in the same direction for

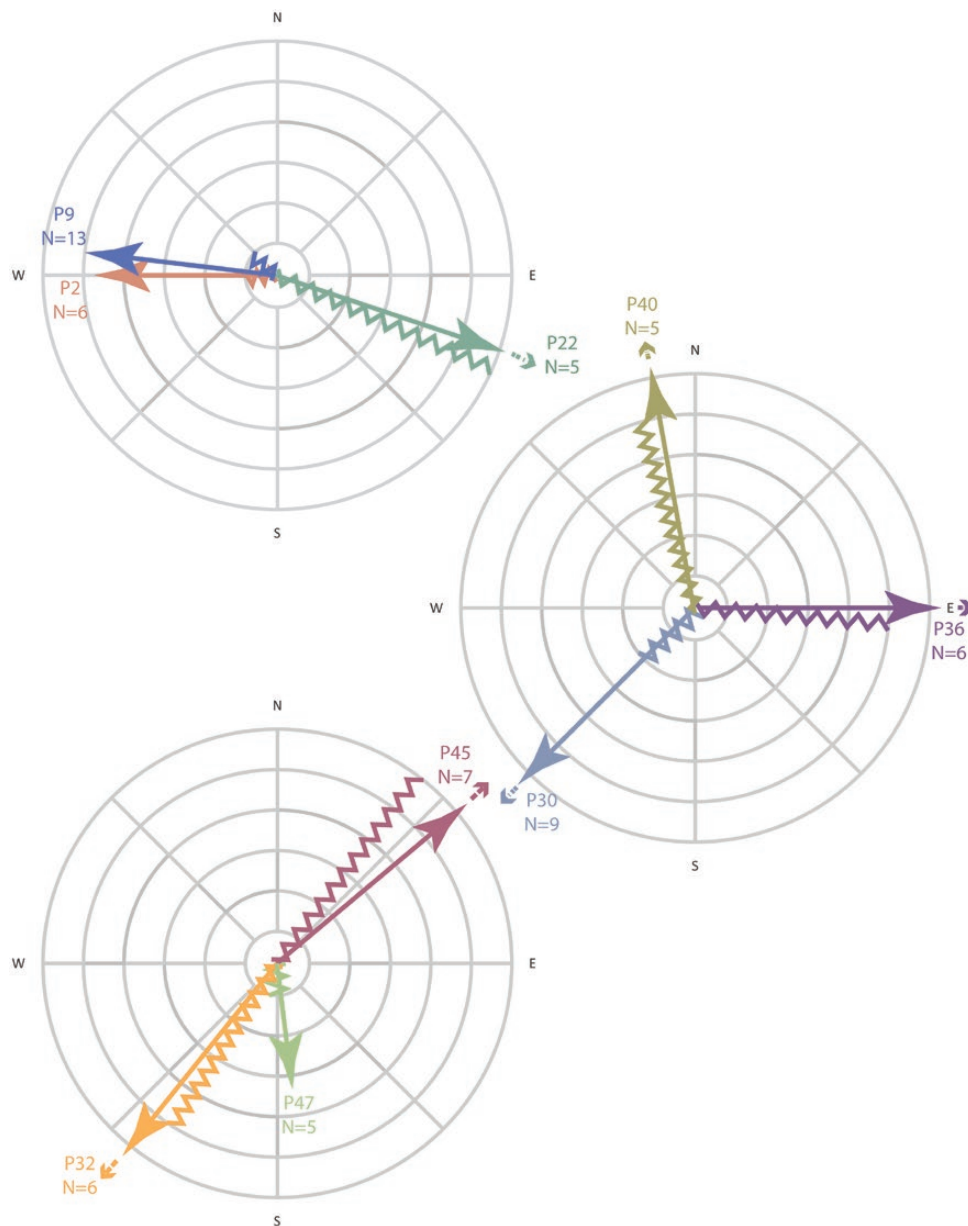


Fig. 8. Compass plots depicting flight directions indicated by dancers, as described in the Materials and Methods, and the following flights of nine bivouacking colonies. Three colonies are represented in each plot, for simplicity. Dances of each worker were numerous and repetitive. Dance angles and duration were virtually unanimous for all dancers in each bivouac (Supp Table S1 [online only]). A zig-zag line of a particular color shows the mean dance angle and dance duration for a colony, with each concentric circle representing 1 s of dancing—waggle runs only for dances of ≥ 3 s duration, complete circuits for dances of ≤ 2 s. Straight lines of the same color show the subsequent flight direction of that colony, with each concentric circle representing 30 m of flight. Most flights exceeded 180 m and disappeared from view, as indicated by broken lines tipped by small arrows. At periphery are identification numbers, beginning with 'P', of bivouacs. N = maximum number of bees simultaneously dancing 30 min before flight.

a particular colony. The bees released, in squirts, minty-smelling feces that were largely liquid, usually colorless or lightly tinged with yellow, as opposed to the usual more solid, yellow-orange feces of nesting bees.

Bivouacking bees were adept defenders. At the BCSS they were regularly harassed by *Vespa* spp. hornets, whose approach elicited shimmering defensive behavior (Kastberger et al. 2011) and rarely resulted in successful predation. The bees also warded off *O. smaragdina* ants quite easily, approaching intruding ants in walking phalanxes and in flight, sometimes using their mandibles to attack and dismember the ants. After ant attacks bees sometimes gnawed at lichens and tree bark where the confrontation occurred, possibly

a response to remove a marking or trail pheromone left by the ants (Fig. 11). The bees shimmered in response to various movements, including flying birds, flying insects such as hornets and butterflies, the passing of motor scooters and bicycles, and the close approach of people. If a person persisted in approaching, the shimmer might be accompanied by a hissing sound. As the response escalated, a 'tail' of bees descended from the bivouac bottom. Defenders might then depart from the tail to sting the intruder, but usually only after all these warning signs were given.

Just as nesting bees do (Thapa and Wongsiri 2015), all but the most rapidly transient bivouacs left small specks of white beeswax behind on the tree bark when they departed, marking the place

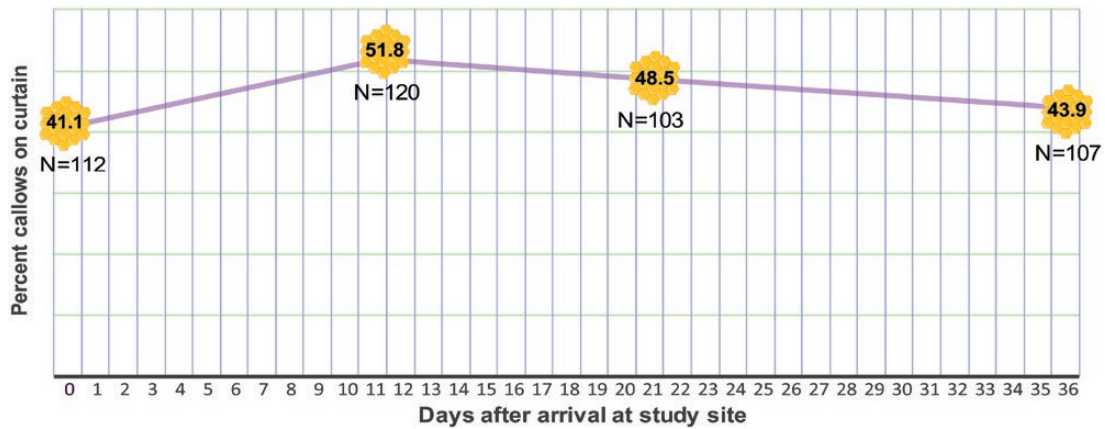


Fig. 9. Line chart showing percentage (inside comb symbols) of callow bees visible on the bivouac curtain in photographs taken at intervals during Bivouac P26's 42-d stay on the study site. Chi-squared tests accepted the null hypothesis that the proportion of callow bees did not differ over the study interval ($P > 0.1$ for all individual comparisons between days; see text).



Fig. 10. A gobbeing worker exposes a droplet of water or dilute nectar to the air, helping to cool her bivouac through evaporation.



Fig. 11. Defending bees gnaw at lichens and bark after an attack by *Oecophylla smaragdina* ants. In the foreground an ant carries off another ant wounded by bees during the attack.

where they had perched (Fig. 12). For bivouacs that remained for long periods of time, these specks were extensive, tracing the slow shifting of a bivouac along its branch with time.

Discussion

Bivouac Features

The most salient result of this research is the strong year-to-year fidelity that migrating bees showed to the BCSS, both spatially and temporally. Bivouacking bees occupied almost precisely the same geographical area in 2016 as in 2009 and 2010. Timing of the stopovers was also remarkably similar, especially to that which Robinson (2012) observed in 2010. (In 2010 the first bivouac arrived 22 September, and field work was terminated with 5 bivouacs still at the site on 19 November; in 2016 occupation of the site lasted from 18 September to 18 November.) These observations provide robust support for the hypothesis that for numerous colonies of *A. dorsata* this BCSS is a regular resting site along the path of an annual migration, with the Pai River serving as corridor, landmark or both. It also continues to be the only such stopover site described by researchers.

The range in sizes of bivouacs was marked in 2016, though lacking the extremely large bivouacs (estimated $>100,000$ bees) of 2010 (Robinson 2012). It appears that as the dry season and accompanying food dearth approaches, many colonies depart their nest sites regardless of the population size they have attained. Migration may in fact be an especially viable strategy for small colonies that cannot compete with larger colonies, which may have the ability to gather sufficient food by expanding foraging territory without migrating (Hepburn 2011).

Colonies chose resting sites much like those Robinson (2012) witnessed. Mango trees, with their shady canopies and rough-barked, upward-angled branches were preferred. Macadamia, and riverside trees of the family Fabaceae also were commonly accepted. Bees were clearly not searching for, and then rejecting, nesting sites; only one colony of 50 built comb in the study site, then abandoned it after 15 d. The 49 bivouacs built no comb whatsoever. In comparison, researchers at an established nesting site in Thailand witnessed many colonies building and then abandoning combs (Dyer and Seeley 1994).



Fig. 12. White beeswax specks above bees clinging to a mango branch mark where the outer curtain of bees had hung in the past. Note mixture of young and older bees.

There was great variation in duration of stay of the bivouacs, just as [Robinson \(2012\)](#) found. This raises puzzling questions that merit further study. If rest and refueling is the presumed purpose of stopovers, why would some bivouacs depart only a few hours after arrival? Why would such colonies bother to stop at all? Why would others stay for many weeks, some foraging vigorously, others spending much of their time quiescent with little foraging?

Another mystery regarding bivouacking bees' behavior is the frequency of periodic mass flights ([Woyke et al. 2004](#)), during which mass defecation invariably occurs ([Robinson 2012](#)). These flights should not be necessary for elimination of wastes from pollen digestion, as bivouacking bees are neither collecting nor ingesting pollen, nor rearing larvae that require it. Nor—obviously for bivouacs—is the frequency of mass flights correlated with the amount of brood present, as [Woyke et al. \(2004\)](#) hypothesized for nesting bees. I frequently saw mass flights by bivouacs that had arrived at the site only hours before. Although [Mardan \(1989\)](#) presented much evidence that defecation flights by bees on comb were thermoregulatory—a means of heat shedding—their occurrence at all times of day once colony activity begins, at both relatively cool and hot ambient temperatures, argues against this hypothesis for the bivouacs studied. In particular, the flights do not appear to be an 'emergency' shedding of heat, as [Oldroyd and Wongsiri \(2006\)](#) hypothesized for bees on comb.

Migration Dances and Flights

Just as [Robinson \(2012\)](#) found in 2009 and 2010, bees in 2016 departed from the BCSS in assorted compass directions, apparently moving out of the Pai River valley to the higher elevations surrounding the study site on all sides. Dances preceding the departures accurately indicated the direction of impending flights. As [Robinson \(2012\)](#) reported, short flights (≤ 150 m) that could be observed in their entirety were preceded by short (≤ 2 -s circuit) dances. This suggestion of a relationship between dance duration and flight distance contrasts with the results of previous researchers, who concluded that for *A. dorsata*, *A. mellifera*, and *A. m. scutellata*, in bees departing from comb, there was no correlation between migration dance duration and distance of flight ([Dyer and Seeley 1994](#), [Schneider and McNally 1994](#), [Lewis and Schneider 2008](#)).

Worker Longevity

[Oldroyd and Wongsiri \(2006\)](#) offered several hypotheses regarding how migrating *A. dorsata* colonies might so precisely find their way back to natal nest sites. They discarded the possibilities that long-lived queens might lead their swarms, or that the colony was simply attracted by the odor of its old, abandoned comb. Their favored hypothesis was that colonies followed a set of 'standard rules' of navigation that resulted in a migration path that often returned them to a previous site, guided by landmarks, local environmental conditions and immediate cues such as tall trees. However, they also entertained the possibility that some worker bees live long enough to retain knowledge of a previous nest site and are able to guide their colonies on a return trip.

Noting that the average lifespan of *A. dorsata* workers under field conditions is simply unknown, [Hepburn \(2011\)](#) dismissed as 'entirely gratuitous' the assumption that no workers could live long enough to serve as guides to a former nest site. It is intriguing that in my series of photographs of a bivouac that remained for 6 wk, I recorded among a large percentage of curtain bees no sign of the metasomal darkening that accompanies aging. I also saw no diminution in volume of any bivouacs, which would be expected if bees were dying of old age. Although [Robinson \(2012\)](#) did not report taking sequential photos of bivouacs in 2009 or 2010, it is noteworthy that one bivouac in 2010 remained in the area for more than 8 wk, and another remained 6 wk. [Robinson \(2012\)](#) reported no attenuation in size of bivouacs.

Two teams of researchers ([Otis et al. 1990](#), [Chinh et al. 2004](#)) found that nesting adult *A. dorsata* workers, associated with larvae, lived a maximum of 2–3 mo. But [Otis et al. \(1990\)](#) also found that caged bees that stopped rearing brood lived longer than those not caring for larvae. These bees also slowed their color transition from callow yellow to orange and black. Broodless, bivouacking giant honey bees may be comparable physiologically to long-lived, wintering *A. mellifera* workers in temperate climates. Most *A. mellifera* workers die within 1–2 wk of their first foraging flight ([Free and Spencer-Booth 1959](#), [Visscher and Dukas 1997](#)). After ~3 wk of hive duties, summer workers thus have a total adult lifespan of ~4–5 wk. However, when pollen sources dwindle, and brood-rearing, production of brood pheromone ([LeConte et al. 1990](#)), and foraging cease for the winter months, workers enter a long-lived winter or 'diutinus' stage ([Amdam and Omholt 2002](#), [Mattila and Otis 2007](#), [Smedal et al. 2009](#)). Diutinus workers commonly survive for 20 wk ([Maurizio 1950](#)), or even for as long as 8 mo or more ([Fukuda and Sekiguchi 1966](#), [Amdam and Omholt 2002](#)). Winter, broodless workers have low titers of juvenile hormone in the hemolymph ([Huang and Robinson 1995](#)) in contrast to the gradually rising titers of the hormone in aging, active workers that are experiencing age polyethism ([Seeley 1995](#)). Diutinus bees also have relatively high titers of the yolk precursor vitellogenin ([Amdam et al. 2004](#)) which can act as an antioxidant to slow aging ([Seehuus et al 2006](#), [Huang and Wang 2015](#)).

Bivouacking, golden-colored, quiescent *A. dorsata* callows might thus be very long-lived and might not change color to the orange and black of foragers until comb-building, brood-rearing, and pollen collection resume. This gradual aging and increased lifespan may be an important and even predictable ([Dyer and Seeley 1986](#)) difference between open-nesting tropical *A. dorsata*—whose workers spend much of their lives in migration and in simply forming a protective curtain over the open nest—and the cavity-nesting *A. mellifera* workers, which assume different tasks in the presence of brood as they age. Another factor that may add to the lifespan of giant honey bees is that, like other

tropical *Apis* species (Ruttner 1988, Radloff et al. 2011), they cease pollen collection and brood rearing well in advance of migration (Punchihewa et al. 1990). Absence of brood pheromone and associated nursing has been shown to cause diutinus status in *A. mellifera* (Amdam and Omholt 2002, Amdam et al. 2004). A brood pheromone might work similarly in *A. dorsata*.

It thus seems plausible that *A. dorsata* workers could live long enough to retain memories from months earlier, and perhaps recall a migration route. If honey bees can form mental maps of their foraging environment (Menzel et al. 2005), might they not also form mental migration maps?

Longevity, rate of aging and specific details of color change in both nesting and migrating *A. dorsata* invite much further study. My means of categorizing callows is admittedly preliminary and somewhat subjective. The use of darkening hairs on metasomal tergites as an index of aging requires further substantiation by paint-marking young bees of known age, or other techniques. Examination of juvenile hormone and vitellogenin titers in migrating workers might reveal much about the rate of aging in these bees.

Functions of the Stopover Site

Migrating animals that utilize stopover sites are presumably resting and refueling, stoking energy reserves for further movement. Honey bees must collect sufficient reserves not only to continue migration but also to construct energetically expensive wax combs at their eventual nesting destination. In Thailand's hot climate, bivouacking honey bees on the curtain spend considerable time gobbling and fanning their wings for evaporative cooling, and thus also require a water source. This BCSS not only features nectar-yielding plants—specifically teak and *Eucalyptus*—but is along a large river that provides water. The river and its steep valley could serve as readily recognizable migratory landmarks, or as a corridor. Mango trees and certain other nearby species provide canopies with shade and branches that are apparently angled to suit the bees' preferences.

Migration Pattern Questions

These and Robinson's (2012) results indicate the colonies at the BCSS are engaged in both short and long flights out of the Pai River valley, in various compass directions into higher-altitude forest that surrounds the study site on all sides. This variety of distances and directions may indicate at least some of the colonies are temporarily nomadic, i.e., they visit various nectar-yielding sites as they make their way in multiple flights, perhaps with some favored stopovers, to thus-far-unknown endpoints for comb-building and nesting. Hopefully, small, honey-bee-compatible geolocators may soon be available to help elucidate migration pathways.

Exploration for Stopover Sites and Their Conservation

Pollinators of many species are in decline world-wide, even as the need for their services increases (Gallai et al. 2009, Partap 2011, Dicks et al. 2016, Potts et al. 2016, Zattara and Aizen 2021). An ever-growing human population exerts demands for insect-pollinated crops, and natural ecosystems are increasingly threatened. The nonagricultural plants of these ecosystems also frequently require insect pollination. Insect pollinators are thus critical to biological diversity and ecosystem stability (Potts et al. 2010, 2016).

Sihag (2014) noted a drastic decline in *A. dorsata* colonies over a 30-yr study of a northern India site. Ahmad et al. (2003) reported severe decline of *A. laboriosa* numbers in Nepal. My conversations with honey vendors and others acquainted with honey-hunting activity in

Thailand indicate that *A. dorsata* populations there are threatened. However, numerical data on the apparently dwindling numbers of colonies are generally lacking (Oldroyd and Wongsiri 2006, Oldroyd and Nanork 2009). Although the Thailand BCSS is the only such stopover site described to date, such sites almost certainly play an important role in supporting the life history and survival of this migratory species, just as they do in bird, ungulate and other insect species such as monarch butterflies (*Danaus plexippus*) (Brower et al. 2006) and the dragonfly *Pantala flavescens* (Anderson 2009).

If stopover sites regularly occur along waterways, as seems likely, they may have already been destroyed in large numbers by riparian tree removal and agricultural development. Destruction or degradation of a stopover site could result in the death of famished or exhausted migrating colonies in need of resting and refueling. Death of older bees in those colonies that have a mental map of the migratory route might eliminate the waypoint or extinguish the migration entirely (Wilcove 2008, Jesmer et al. 2018, Satterfield et al. 2020).

Specifically, this unique BCSS in northern Thailand deserves permanent protection. This takes on added importance considering Robinson's (2013) report that numerous swarms of absconding *Apis cerana*, the eastern hive bee, also occupied the mango orchard in 2009. Remarkably, Robinson (2011) also studied the black dwarf honey bee, *Apis andreniformis*, in the same small orchard. The site's status as part of the Mae Hong Son Agricultural Research and Development Center should make its preservation achievable.

Meanwhile, researchers should search for more such sites, which undoubtedly exist in places where giant honey bees migrate. To begin, I suggest searching along rivers—major landmarks or guides—between well-known nesting sites at the times of year when bees are known to be on the move. There may be a role for citizen science in such searches, as there has been with monarch butterflies in the United States (Davis et al. 2012). Studies should also be conducted on bees' preferences for resting sites, and whether rafters of certain sizes and textures, positioned at particular angles, might attract bivouacs. The bees in this study preferred branches tilted on average at a 45° angle above horizontal, but with wide variation; giant honey bees seeking nesting sites apparently prefer rafters tilted 10–30° above horizontal (Tan et al. 1997, Chutrong et al. 2019).

When technically feasible, research using geolocators should be conducted to clarify specific giant honey bee migration routes. That research could in turn enable policy makers to take steps to protect the vital migratory routes of these spectacular, charismatic pollinators and honey producers as they 'surf the sweet wave' of changing nectar availability.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Acknowledgments

I dedicate this study to the memory of Dr. Jaroon Kumnuanta, former chairman of the Mae Hong Son Community Foundation, and a stalwart, serenely moral pillar of the Mae Hong Son community. A dear friend to my wife and me, Jaroon facilitated every aspect of my research. I thank my wife, Maria Katherman, for extensive technical support and sound thinking about the puzzles of honey bee migration. Natthanon Fusang, Director of the Mae Hong Son Agricultural Research and Development Center, facilitated access to the center and lent enthusiastic support for the project. Yotin Boonchalay and Jesseda Weera helped with logistical problems of the research and provided constant friendship. A private citizen, Dr. Gail Zimmerman, provided funding for transportation and housing. Julie Hansen and Quinn Robinson prepared

the figures for this paper. Dr. Gard Otis (University of Guelph) and Dr. Zachary Huang (Michigan State University) reviewed the manuscript and provided invaluable comments prior to submission.

Author Contributions

W.S.R.: All contributions of this article done by single author.

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