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Timing of drone flights and observations of other colony behaviors of *Apis laboriosa* in northern Vietnam

Hanh D. PHAM¹, Chinh H. PHUNG², Dien T. BUI³, Lam D. NGUYEN³, Thanh T. NGUYEN³,
Karen J. HAND⁴, and Gard W. OTIS^{5,6} 

¹ Dong Da District, Chua Lang St, No 4, 121 Lane, Hanoi, Vietnam

² Mountain Bee Development JSC, Khuong Trung St, Thanh Xuan District, 54/211 Alley, Hanoi, Vietnam

³ Center for Bee Research and Animal Technology Transfer, 175 Van Phuc Road, Ha Dong District, Hanoi, Vietnam

⁴ Precision Strategic Solutions, 142 Hume Rd, Puslinch, ON N0B 2J0, Canada

⁵ School of Environmental Sciences, University of Guelph, Guelph, ON N1G 2W1, Canada

⁶ Institute of Bee Health, Vetsuisse Faculty, University of Bern and Agroscope, CH-3097 Bern, Switzerland

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Abstract – We studied an aggregation of *Apis laboriosa* colonies in northern Vietnam where the species is sympatric with *Apis dorsata*. We video-recorded four colonies on 2 days to quantify drone flights and other colony behaviors. We observed > 90% of drones between 16:10 and 18:10 h ICT, with the maximum numbers between ~ 17:10 and 18:00 h. Drone flight timing did not differ between days or between colonies. Aggressive worker behavior toward some arriving drones suggests considerable drifting of drones between nests. Massed flight activity, a colony behavior in which a high proportion of bees temporarily leaves the comb, occurred in several colonies between 14:00 and 16:40 h. We also documented absconding by one colony. *A. laboriosa* drones ended their mating flights before the typical mating flight time of *Apis dorsata* at evening twilight. We conclude that allochrony of mating is a likely reproductive isolating mechanism between these two species of giant honey bees.

Drone / Mating flight / Reproductive isolation / Giant honey bee / Absconding / Massed flight activity

1. INTRODUCTION

The giant honey bees, represented by two–five Asian species (Oldroyd and Wongsiri 2006; Smith 2021) in the genus *Apis*, construct large, single-comb nests that are covered by a living curtain of worker bees (Seeley 1985; Oldroyd and Wongsiri 2006). *Apis laboriosa* Smith 1871, the world's largest honey bee (Sakagami et al. 1980), occurs across the Pan-Himalayan region, from northern India to northern Vietnam (Kitnya et al. 2020),

where colonies nest at relatively high elevations (in Nepal, usually at 2500–3200 masl; in north-eastern India and northern Vietnam, between 800 and 1500 masl) (Roubik et al. 1985; Kitnya et al. 2020). It is replaced by *A. dorsata* Fabricius, 1793 in tropical and subtropical regions of Asia (Sakagami et al. 1980; Hepburn and Radloff 2011; Smith 2021; iNaturalist 2023). Both species frequently nest in aggregations, *laboriosa* almost always on rock cliffs and *dorsata* typically on tall trees, water towers, and other high structures, but also on rock faces (Phiancharoen et al. 2011; Lam et al. 2022). The two species are partially sympatric in parts of northeastern India (Sakagami et al. 1980; Kitnya et al. 2020, 2022), northern

Corresponding author: H. D. Pham, hanhbees@yahoo.com;

G. W. Otis, gotis@uoguelph.ca

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Vietnam (CHP and HDP, pers. obs), and likely other locations.

As a consequence of the physical settings in which giant honey bees build their nests and their strong colony defense, getting close to colonies for both observation and experimentation is difficult, and therefore many aspects of their biology remain poorly known (Morse and Laigo 1969; Seeley et al. 1982; Underwood 1990a). The surface of the comb as well as the queen, brood, and many activities of worker bees are obscured under several layers of worker bees that compose the protective bee curtain. Drones are also usually hidden from view; they become visible only when they undertake flights from a colony or when large numbers of worker bees temporarily fly *en masse* from a nest and expose much of the comb surface.

Because *A. laboriosa* lives at high elevations in remote mountain locations, few specimens have been available for study until relatively recently. Consequently, besides its initial description (Moore et al. 1871) and brief mention by von Buttel-Reepen (1906) and Cockerell (1914), *A. laboriosa* was neglected until Maa (1953) provided a detailed description of it among the 24 species he recognized in his revision of the honey bees. Due to his excessive splitting of taxa, Maa's treatise on *Apis* was poorly accepted and many bee taxonomists have considered *A. laboriosa* to be a large subspecies of *A. dorsata* (e.g., Michener 1984; Ruttner 1988, 1992; Engel 1999). However, following their detailed morphological study of giant honey bees, Sakagami et al. (1980) concluded that "this long ignored, magnificent form is specifically different from *dorsata*." Subsequent morphometric analyses (Cao et al. 2012; Kitnya et al. 2022), genetic analyses (Arias and Sheppard 2005; Raffiudin and Crozier 2007; Lo et al. 2010; Le 2013; Kitnya et al. 2022), chemical differences (Carlson et al. 1991; Blum et al. 2000), as well as several other differences (Radloff et al. 2011) strongly support the distinctiveness of *A. laboriosa* from *A. dorsata*, as was recognized by Michener (2000). Contrary to that view, the male endophallus, a complex structure that often differs between honey bee

species, does not conclusively differ between the two taxa (McEvoy and Underwood 1988; but see Koeniger et al. 1990). In the last major taxonomic review of the genus *Apis*, Engel (1999) left unresolved the question of species-status of *A. laboriosa* by concluding, "My decision to place *laboriosa* within *dorsata* should be examined more closely" as new information is obtained.

For *A. laboriosa* to be a species distinct from *A. dorsata*, the two taxa must be reproductively isolated from each other where they occur sympatrically. Koeniger and Koeniger (2000) summarized the various traits of honey bees that operate to prevent interspecific mating. One of the most important pre-mating barriers between *Apis* species is allochrony of mating flights. Drones and queens of all honey bee species leave their colony and mate in the air. The temporal distributions of these flights usually differ among sympatric species (Otis et al. 2000, and references therein; Oldroyd and Wongsiri 2006). McEvoy and Underwood (1988) suggested that in the absence of differences in their male reproductive organs, differential timing of mating flights of *A. laboriosa* and *A. dorsata* may provide a barrier to interspecific mating. Underwood (1990b) provided preliminary data suggesting that *A. laboriosa* mating flights occur in early afternoon in Nepal. In contrast, it has been well-documented widely across Asia that *Apis dorsata* drones initiate their mating flights close to or after sunset, in Sri Lanka (Koeniger and Wijayagunasekera 1976); southern India (Woyke et al. 2005, 2007); Borneo (Koeniger et al. 1988, 1994; Beaurepaire et al. 2014); southeastern Thailand (Rinderer et al. 1993); southern Vietnam (Tan et al. 1999); Sulawesi, Indonesia (Otis et al. 2000); and Luzon Island, the Philippines (Woyke et al. 2005). Some researchers consider *A. d. binghami* of Sulawesi and *A. d. breviligula* of the Philippines to be distinct species (Maa 1953; Raffiudin and Crozier 2007; Lo et al. 2010). Koeniger and Koeniger (2000) emphasized that Underwood's (1990b) observations need to be confirmed.

Quantifying the timing of mating flights of honey bee drones is not simple because they fly from their nest for reasons other than

mating (summarized by Reyes et al. 2019). In *Apis mellifera*, the first few flights adult drones undertake are orientation flights that are usually shorter in duration than mating flights (Howell and Usinger 1933; Witherell 1971 and references therein; Reyes et al. 2019 and references therein; Woodgate et al. 2021). Tracking young drones with harmonic radar shows that these flights consist of several loops in different directions within ~130 m of their colony (Woodgate et al. 2021). Orientation flights enable drones to learn the location of their nest in the landscape (Hayashi and Satoh 2021; Hayashi et al. 2022) as also occurs in worker bees (Capaldi et al. 2000; Degen et al. 2016). There have been no studies of orientation flights of giant honey bee drones. Additionally, both drones and worker bees need to defecate, which they almost always do in flight away from their nest (Seeley 1985). Finally, drones may leave their nest during colony defense. Unfortunately, without being able to track individual flights of drones, it is impossible to determine their function. Because drone flights of most species of honey bees occur during discrete periods of the day, nearly all researchers have simply referred to all drone flights as “mating flights.”

Drone flights of giant honey bees are further complicated by the colonial behavior known as massed flight activity (MFA; also referred to as “periodic mass flights” and “colony en masse airborne”; see descriptions by Kastberger et al. 1996; Woyke et al. 2003). During MFA, the regular vertical orientation of worker bees in the external bee curtain is disrupted as bee activity gradually increases. Then, after some minutes, a large number of bees leave the comb, fly in the air in the vicinity of the nest, and then return to the comb. Worker bees often defecate during MFA (Ashton et al. 1983; Mardan and Kevan 1989), and it is likely that drones do as well. Learning of landmarks surrounding the nest (i.e., orientation) also likely occurs during those same MFA events (Woyke et al. 2004, 2007). MFA events occur at various times during the day, even at dusk (Woyke et al. 2007) when mating flights of *A. dorsata* queens have been observed (Tan et al. 1999).

We recently learned of two sites in extreme northern Vietnam where *A. laboriosa* colonies consistently build their nests on readily accessible cliffs. In May of 2021, we visited them and discovered that the low height of the nests at one site would enable us to observe and video-record colonies, thereby allowing us to quantify departures and arrivals of drones. While video-recording colonies, we also documented several MFA events and one migratory absconding event.

Here, we confirm that *A. laboriosa* males in northern Vietnam take most of their flights, most of which are mating flights, in the late afternoon but earlier than when *A. dorsata* drones have been documented to take mating flights. These observations provide the best evidence to date that *A. laboriosa* and *A. dorsata* are reproductively isolated by allochrony of mating times.

2. MATERIALS AND METHODS

2.1. Methodology

Our study was conducted at a cliff with 30 active *A. laboriosa* colonies (Figure 1) located in extreme northern Vietnam (Quang Thanh commune, Nguyen Binh District, Cao Bang Province; 22°35'21" N, 105°55'10" E; 880 masl), from 5–7 May and 6–10 July, 2021. This is the most easterly confirmed nest site of this species. The overhanging cliff protected the nests from rain, but because it faced west, many colonies were exposed to solar radiation during the afternoon. *A. dorsata* occurs sympatrically with *A. laboriosa* in this region: it was known to nest ~3 km from our study site. Local residents harvest beeswax from abandoned combs at the study site after all colonies have absconded; however, they do not disturb the colonies between when they typically arrive and construct nests in February and when they abscond in July. They readily differentiate the two species of giant honey bees on the basis of color differences, as described by Sakagami et al. (1980) and Kitnya et al. (2022), and their usual nesting sites (*laboriosa* = “rock bee”, *dorsata* = “tree bee”).



Figure 1 Photograph of the aggregation of *A. laboriosa* colonies at the study site in Quang Thanh commune, Nguyen Binh District, Cao Bang Province, Vietnam. The relative sizes of the nests, their different orientations, and their proximity to each other are evident.

On our first visit to the nest site in May, we took photos and preliminary videos of the colonies and of the site to plan our activities. We

selected four colonies centrally located within the nest aggregation that were oriented approximately perpendicularly to the line of sight from a

suitable observation location. We video-recorded those nests on the afternoons of 7 and 9 July, with Sony video cameras (three HDR-CX405 and one HDR-CX290 model cameras), using the same camera for each colony on both days. Rain on 8 July prevented observations. Each video camera had a 64 GB memory card and two spare batteries, except for video camera #3 (Nest 3) for which we used two 32 GB memory cards and video camera #4 (Nest 4) for which there was only one spare battery. The distances from the cameras to the selected nests, measured with a Bosch GLM 500 laser distance meter, were 16.9 m, 14.8 m, 13.8 m, and 13.2 m for Nests 1 to 4, respectively.

All four video cameras were set to the highest magnification of their optical lens (60 \times for the HDR-CX405 model and 50 \times for the HDR-CX290 model). At those magnifications, bees were sufficiently large in the videos to be identified to caste, but only the central portions of the selected colonies could be recorded. Minor gaps in recording (30–60 s) occurred during quick changes of batteries and memory cards.

On the first day of video recording, 7 July, the weather was favorable, with temperatures ranging from 25 to 34 °C and alternating sunny and cloudy periods, except during ~ 10 min from 12:40 to 12:50 h when clouds associated with nearby rain darkened the sky. We recorded three colonies continuously from shortly after noon until ~ 15 min after drone flights ceased; at Nest 4, the camera stopped recording at 16:23 h when the batteries died.

On 9 July, heavy rain fell from 05:00 to 07:00 h, followed by scattered showers, heavy overcast, and fog throughout the morning. The temperature over that day varied between 24 and 31 °C. The rain ended at 12:00 h and the sky quickly brightened, with sun and scattered clouds prevailing soon after the rain ended. A brief rain shower occurred from 15:25 to 15:45, after which scattered sun and clouds returned for the remainder of the day. We video-recorded the four colonies from approximately 14:00 to 18:30 h. Once again, the batteries in the camera recording Nest 4 failed before the drone flight had ended, at 17:22 h. Supplementary Table S-I

provides the details of the cameras and periods of recording at the four nests over the 2 days.

To extract data on the number and timing of drones leaving and returning to nests from video clips (Supplementary Table S-II), DTB reviewed all videos 2–3 times. For bees that were difficult to identify to caste, he viewed videos slowly backward and forward until those bees were either clearly identified as drones and could be included in the data or they were ignored. HDP and CHP spot-checked bees identified as drones in the videos for accuracy. Because some drones were treated aggressively by worker bees upon landing and numerous drones departed again soon after landing, we separated the returning drones into two groups: 250 drones that departed again within 30 s and 1004 drones that landed and moved out of sight below the bee curtain. Behavior of workers toward drones was also noted.

The videos also enabled us to collect data on massed flight activity (MFA) and absconding. During our observations of nests, we detected and noted the times of several instances of large numbers of worker bees flying off their nests in what corresponded to descriptions of MFA (Kastberger et al. 1996; Woyke et al. 2003). The video-recordings of these events were viewed repeatedly to determine the timing of MFA events (e.g., the times when the vertical orientation of bees in the curtain began to become disrupted, when large numbers of bees were absent from the comb, and when the bees were once again calm and oriented vertically) and the numbers of drones departing and returning to combs during them. One colony absconded while we were present, which enabled us to quantify the timing of events associated with absconding.

Because drones were unmarked and the video cameras were focused on only the central portion of one side of each nest, we could not quantify the timing and behavior of individual drones. Therefore, we could not differentiate drones on mating flights from those making orientation or defecation flights. As we witnessed no colony defense, drone flights associated with worker attacks on intruders did not contribute to the data.

We report the times of drone flights and colony events in local Vietnamese (ICT) time. Solar time at the study site differed only slightly from local time: solar noon occurred 1:25 min after ICT noon (NOAA 2022). Sunset occurred at 18:45 ICT on 7 and 9 July (NOAA 2022).

2.2. Statistical analyses

The numbers of drones arriving at nests were grouped into 20-min intervals (variable “interval”), beginning at 12:30 h and ending at 18:30 h ICT. The data were coded by “colony” (Nest 1 to 4) and “day” (7 July = Day 1; 9 July = Day 2). We did not include in the statistical analysis the data obtained during time intervals when the video-cameras were not activated and those for which the video-recordings were incomplete, with one exception: during the interval from 17:10 to 17:30 h for Nest 4 on 9 July, recording ended at 17:22 (i.e., the recording covered 60% of the time interval). The model was used to estimate drone arrivals for the full 20-min interval based on the numbers observed during the first 12 min (i.e., 60% of the time interval).

Drone activity was low until 16:10 h, then showed a pattern over the remainder of the afternoon (Figure 2) typical of drone mating flights documented in the literature for many species of honey bees (e.g., Rinderer et al. 1993). Consequently, we divided our analysis into two flight “periods”—period 1 (12:30–16:10 h) and period 2 (16:10–18:30 h). Most massed flight activity (i.e., six of seven MFA events) occurred late in period 1, not during period 2 when the flights likely to be mating flights occurred.

All analyses were conducted using SAS version 9.4 (SAS Institute). The response variable was defined as the number of drone arrivals per 20-min interval. The data were modeled using PROC GENMOD, assuming the negative binomial distribution. The independent variables included class variables for colony, day, and flight period, and the qualitative variable, interval (i.e., the 20-min interval in which drone arrivals were counted). All interactions were considered as well as linear and quadratic

effects of interval. Using a stepwise approach, non-significant effects were eliminated from the model using likelihood ratio tests for type 3 analysis. Residual analyses were performed on all models (i.e., plotting residual by predicted response and residual by each independent variable) to assess data anomalies (including outliers), of which there were none. The model was not able to include a covariance structure resulting from correlations in the data between successive observations due to lack of replication. SAS PROC GENMOD generated LS Means to estimate median drone arrival rates, and 95% confidence intervals for each time interval by colony by flight period; we also used PROC GENMOD to conduct paired difference tests to detect significant simple effects.

3. RESULTS

3.1. Drone flights

We detected more drones returning to their nests than departing (in Nests 1–3, for which our video-recordings covered the time from first to last drone flights: $n = 1004$ versus 384; in Nest 4, for which data for the time intervals late in the afternoon were missing: $n = 342$ versus 240). Drones preparing to depart on flights appeared individually from under the curtain of bees, typically with no apparent interactions with nearby bees. Most (~70%) drones that emerged from the bee curtain crawled onto the bodies of workers for 1–3 s, then took flight. However, some (~10%) were treated aggressively by surrounding workers. In other instances (~20%), we saw only the drone head, evident from its large eyes, among worker bees in the bee-curtain before it rapidly flew off. Because such drones were inconspicuous, we believe that we failed to detect some of them in the video recordings before they departed.

Upon their return, the majority (80%) of drones joined the colony while others (20%) took flight again. Among those that joined nests, ~85% landed on the curtain of worker bees and walked about for several seconds with their wings opened at a ~45° angle prior

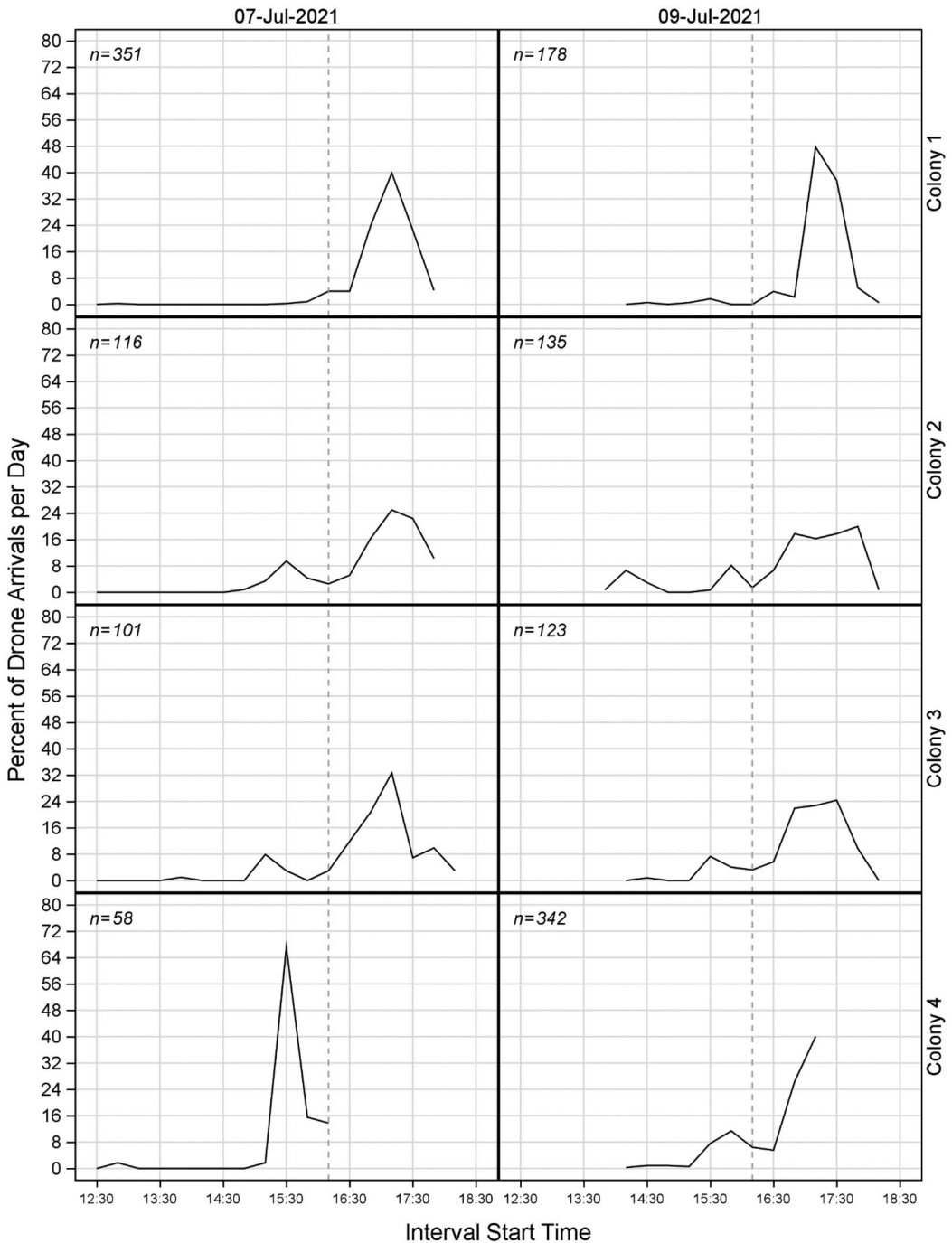


Figure 2 Proportions of drones observed landing on four *Apis laboriosa* colonies, Cao Bang Province, Vietnam. Data were recorded in 20-min time intervals on 7 and 9 July, 2021. Sample sizes for each graph are shown in the upper left corner. The vertical dashed lines separate period 1 and 2 in the statistical analyses. The last values shown on the graphs for colony 4 are estimates based on the assumption that the rate of returning drones in the recorded portion of the time interval continued to the end of the time interval. The relatively large number of drones arriving between 15:30–15:50 h at colony 4 on 7 July correspond to mass flight activity.

to disappearing under the curtain. Other drones (~ 15%) flew to the nest and disappeared quickly under the bee curtain (comments on behavior in supplementary file S-III). Because arriving drones were (i) generally visible on the nest surface longer than departing drones, (ii) more readily detected in the videos, and (iii) reported by Underwood (1990b), we focused our analysis on drones returning to their nests.

Figure 2 depicts the proportions of drones detected in the video-recordings arriving at each colony on each day during the 20-min time intervals (see also supplementary Table S-III). The first drone flights occurred at approximately 12:30 h ICT (Table I). However, drones were rarely observed before 15:10 h (viz. 18/1004 = 1.8% of drones that returned to and joined Nests 1–3) and only 8.4% (84/1004) of returning drones were recorded before 16:10 h. Additionally, very few drones (5/1004 = 0.5%) returned to Nests 1–3 after 18:10 h, with the latest drone observed at 18:26 h (Table I). Statistical modeling of drone numbers per

interval detected a significant effect of colony ($p < 0.0001$), flight period (before vs. after 16:10 h, $p < 0.0001$), both linear and quadratic effects of interval (20-min time intervals, $p < 0.0001$), the colony by flight period interaction ($p = 0.0006$), as well as both the linear and the quadratic interval by flight period interactions ($p < 0.0001$). The final model and Type 3 likelihood ratio p values can be found in Supplementary Table S-IV and the median estimated numbers of drones arriving at the colonies, as determined by the statistical model, are shown in Supplementary Figure I. The overdispersion parameter was estimated to be 0.545 with a 95% Wald confidence interval of (0.346, 0.858), which supports modeling using the negative binomial as opposed to the Poisson. (The Poisson model is often applied to count data but is most appropriate when the overdispersion parameter approaches zero.) There was a strong simple effect (interaction) of “colony by flight period,” with several pairwise comparisons being significant (Supplementary Table S-V).

Table I Timing of the first and last *Apis laboriosa* drones observed in video recordings as they departed and arrived at colonies on 7 and 9 July, 2021. The data for colony 4 are incomplete on both days because the battery in the video recorder failed before the end of the drone flight. Times are presented in ICT (local Vietnamese time). Sunset occurred at 18:45 h ICT

Date		7 July 2021			9 July 2021		
		Departing drones			Arriving drones		
Colony		First	Last	Peak interval	First	Last	Peak interval
1	7 July	15:38	17:56	17:10–17:30 (14/45 bees)	13:08	18:08	17:10–17:30 (140/351 bees)
	9 July	15:29	17:48	16:10–16:30 (33/85 bees)	14:38	18:26	17:10–17:30 (85/178 bees)
2	7 July	12:25	17:52	16:30–16:50 (12/54 bees)	12:25	18:08	17:10–17:30 (29/116 bees)
	9 July	15:54	18:16	16:30–16:50 (17/52 bees)	14:06	18:16	17:50–18:10 (27/135 bees)
3	7 July	12:28	18:12	17:10–17:30 (16/58 bees)	12:26	18:11	17:10–17:30 (33/101 bees)
	9 July	15:27	17:29	16:10–16:30 (30/90 bees)	14:42	18:04	17:30–17:50 (30/123 bees)
4	7 July	13:06	–	–	13:04	–	–
	9 July	15:29	–	–	14:27	–	–

Surprisingly, despite the rain and heavy clouds on the morning of 9 July, “day” did not affect the timing of flights of drones in our study.

3.2. Drone landing behavior and worker aggression toward drones

Most drones (1004 of 1254 drones detected in videos as they returned to Nests 1–3) landed and, after walking briefly on the bee curtain, disappeared under it within 30 s (i.e., 1–3 s (~40%), 4–10 s (~40%), and the remaining ~20% after 11–30 s; Supplementary file S-II). Occasionally, those drones were licked without evidence of aggression by worker bees. Of the 1004 drones, a small number ($n = 10$; 1.0%) were treated aggressively by worker bees upon their arrival but nevertheless they proceeded to quickly enter under the protective curtain of bees. However, an additional 250 drones, nearly 20% of the 1254 drones arriving at Nests 1–3, took off again within 30 s; of those, 48 (19.2%) were treated aggressively by workers upon their arrival. This aggression took the form of one to six workers attempting to bite the wings, head and/or legs of drones upon landing, causing the drones to shake their bodies strongly. In most instances, these drones departed the nest soon after the aggressive actions of workers.

3.3. Massed flight activity

Several colonies underwent MFA during our afternoon observations. Of the 30 nests at the nest site, we observed MFA at 9 colonies (Nests 1–4 and 5 others) on 7 July and 4 colonies (Nests 1–3 and one other) on 9 July, between 14:00 and 16:40 h. During most of the afternoon, most of the bees in the curtain were oriented vertically and were quiescent. MFA involved workers in the curtain becoming more active (i.e., walking), which began to disrupt their vertical orientation. After 2–9 min, many bees left the nest which made the bee curtain thinner. After flying as much as 10 m from their nest for 2–11 min (mean 6.4 ± 4.1 min), they began to land on the comb again and the

colony returned to a calm state. The total duration of MFA events ranged from 7 to 21 min (mean $= 14.7 \pm 5.2$ min, $n = 7$). We observed only one MFA per colony per day, but we also only observed colonies during the afternoon. During our reconnaissance visit on 6 May, we noted MFA events of several colonies between 12:30 and 13:40 h. Details of the timing of events during MFA are presented in Table II.

3.4. Absconding

When we first visited the study site on 5–7 May, we counted 30 active nests. On our return on 6 July, of the 30 nests, two large and one very small one lacked bees due to absconding. We watched as another colony absconded on 7 July. At 15:14 h, we noticed bees becoming more active and walking on top of other bees in the protective curtain. Gradually their activity increased. After approximately 20 min, we observed coordinated shaking or dancing behavior; however, due to the distance of observers from the nest, we were unable to quantify this behavior in detail. Some bees flew off the nest, then returned to the upper portion of it, which gradually exposed the lower portion of the comb. At 15:45 h, bees began to leave the nest in large numbers. Within a minute, all the bees were airborne and flying approximately 10–20 m from the comb. At 15:48 h, the swarm departed in a westerly (~250°) direction along the long axis of the valley.

Photos of the four combs from which the bees had absconded showed small numbers of scattered sealed brood cells and no stored honey. The three larger combs each had the remains of four queen cells along the lower comb margin, indicating that those colonies had undergone either reproductive swarming or queen superseding after establishing nests earlier in the year.

4. DISCUSSION

We have documented that in northern Vietnam, *Apis laboriosa* drones take the majority of their flights in the late afternoon. More than

Table II Timing of massed flight activity of *Apis laboriosa* on afternoons of 7 and 9 July, in Cao Bang, Vietnam

	7 July, 2021				9 July, 2021				Mean ± SD (min)
	Col 1	Col 2	Col 3	Col 4	Col 1	Col 2	Col 3	Col 4	
1. Time when curtain bees first become restless and vertical orientation of bees began to be disrupted	16:10	15:22	15:20	15:23	16:34	15:25	15:29	–	
2. Time when a large number of bees departed the nest	16:15	15:28	15:26	15:32	16:36	15:27	15:34	–	
3. Time when most of the bees have returned to the nest	16:18	15:39	15:39	15:38	16:38	15:32	15:39	–	
4. Time when the curtain bees were quiet again and most were oriented vertically	16:21	15:42	15:41	15:41	16:41	15:39	15:41	–	
Duration (min) of airborne portion of MFA (2 to 3) (<i>n</i> = 7)	3	11	13	6	2	5	5	–	6.4 ± 4.1
Duration (min) of MFA (1 to 4) (<i>n</i> = 7)	11	20	21	18	7	14	12	–	14.7 ± 5.2
# drones departing (1 to 4)	2	1	3	24	0	0	14	–	
# drones arriving (1 to 4)	4	12	11	34	0	0	5	–	
# drones departing (2 to 3)	1	1	0	6	0	0	2	–	
# drones arriving (2 to 3)	1	9	6	29	0	0	5	–	

90% of drones returned to their nests between 16:10–18:10 h (period 2), with peak numbers generally arriving between ~17:10–18:00 h. We believe that most of the flights in period 2 were mating flights, but because drones could not be followed individually, some may have been orientation and/or defecation flights and we could not designate them as mating flights with certainty. This is actually an issue for all studies that have documented the timing of “mating flights” of drone honey bees: mating versus orientation/defecation flights can only be differentiated with certainty by tracking drones in flight (cf. Woodgate et al. 2021) which is rarely possible.

The timing of drone flights we observed differs strikingly from Underwood’s (1990b) observations of *A. laboriosa* drones in a colony situated at 2680 m on 10 September in Nepal. In that colony, the entire drone flight took place between 12:15 and 14:20 h Nepal standard time (i.e., 12:05–14:10 h solar time). Despite this striking intraspecific difference between colonies in Nepal and Vietnam, drones in Vietnam

nevertheless ended their flights well before evening twilight when *A. dorsata* drones, wherever they have been studied within the range of the species, are known to initiate their mating flights. We discuss this in more detail below.

Studies on *A. mellifera* have demonstrated that the timing of drone flights is influenced by both environmental and genetic factors (Rowell et al. 1986). Environmental conditions, such as temperature, cloud cover, and wind speed influence mating flight times (Alber et al. 1955; Taber 1964). *A. mellifera* drones will extend their flights later into the afternoon if prevented from flying earlier in their flight period (Taber 1964; Oxley et al. 2010; Z. Huang, pers. comm.) or if temperatures are high (Verbeek and Drescher 1984), and will depart earlier after having been confined on the previous day (Ruttner 1966; R. Currie, pers. comm.). The relatively cool temperatures at high elevation in September in Nepal, coupled with frequent afternoon rains, may have caused drones there to adjust their behavior by flying early in the afternoon. In contrast, at our

study site in Vietnam, the afternoon temperature reached a maximum of 34 °C. Drones may have delayed their flights until temperatures began to cool later in the afternoon. Despite the heavy cloud cover and rain in the morning on the second day of our observations, “day” was not a significant variable in our statistical model.

Several studies indicate that drone flight times are also influenced genetically (Oldroyd and Wongsiri 2006). For example, intraspecific differences have been reported previously in the timing of flights by drones of different populations, likely in response to interactions with drones of sympatric species and other local selection factors (Otis et al. 2000; Oldroyd and Wongsiri 2006). In *A. mellifera*, drones from colonies representing different commercial stocks differed in their flight times (Rowell et al. 1986). In our study, despite our only being able to quantify drone flights from four colonies, several pairwise comparisons between colonies did differ significantly (Table S-V), suggestive of genetically caused differences.

A relatively large proportion (~ 20%) of drones returned from flights, landed on nests, then took off again within 30 s. Approximately 20% of those bees that quickly departed had been treated aggressively by worker bees when they landed on the bee curtain. Distances separating adjacent nests in the aggregation were small, < 1.5 m, and in most cases only 0.5–1.0 m (Figure 1). We suggest that the drones that were treated aggressively upon landing as well as many of those that took flight again soon after landing likely had misoriented and landed on a foreign nest. In *A. mellifera*, drifting of drones within apiaries is well documented, can be quite extensive, and is greater than drifting of workers (Currie and Jay 1991; Moritz and Neumann 1996, 2004; Reyes et al. 2019). There are no direct observations or data on drifting of drones between colonies of giant honey bees in aggregations of nests. The only relevant data for giant honey bees come from studies of foreign worker bees in *A. dorsata* colonies nesting in small aggregations, with estimates of percentages of drifted bees that range from 1.3–1.5% (Paar et al. 2000, 2002)

to 11.5% (Moritz et al. 1995). Drones that we observed being treated aggressively may have eventually been accepted by colonies. Unfortunately, with our methodology, we were unable to quantify misorientation and drifting.

We witnessed 13 massed flight activity events by the 30 colonies during our two afternoons of observation. The behavior we observed generally agrees with that described for *A. laboriosa* by Woyke et al. (2003) in Nepal. However, we observed somewhat fewer MFA events per colony and did not record more than one MFA per day, compared to the observations of Woyke et al. (2003). We also did not observe the nests in the morning and therefore almost certainly missed some MFA. All but one MFA that we observed occurred in period 1, prior to when most drone flights occur. In general, we detected few drones participating in MFAs except from Colony 4 during period 1 on 7 July (Figure 2). (Note that the numbers of drones flying from that colony during period 2 later that afternoon were not recorded due to battery failure.) Consequently, we conclude that drones that took flight during MFAs had little influence on the data related to the timing of mating flights.

At our study site near the Vietnam-China border, *A. laboriosa* is a seasonal inhabitant. According to local residents, swarms arrive and construct nests at the study site in February. They are reported to abscond in July. Our observations confirmed that three colonies had absconded prior to 6 July and we watched a fourth colony abscond and fly toward the west-southwest on 7 July. Unfortunately, the destinations of swarms that abscond from our study site are unknown.

The remnants of queen cells on the lower margins of three empty combs suggest that some of the colonies may have reproduced during their stay at the nest site. The numbers of combs was unchanged between our visits to the site, so if colonies swarmed (reproduced) between May and July, the swarms left the site. Alternatively, colonies may have swarmed in March/April, or they may have superseded their queens. We mention this because there is a paucity of information on swarming,

absconding, and associated behaviors of giant honey bees (subgenus *Megapis* spp.).

At a number of sites in northern Vietnam, *A. laboriosa* and *A. dorsata* are partially sympatric at elevations between ~600 and 1200 masl. Local residents informed us that *A. dorsata* nested within 3 km of our study site. Elsewhere in northern Vietnam, foragers of these two species have been observed within a few cm of each other and colonies of the two species have nested ~400 m apart in Van Ban District, Lao Cai Province (CHP and Dinh T. Nguyen, pers. comm.). During our observations of *A. laboriosa* colonies in Vietnam, the flight period of drones in the four colonies ended 19–41 min before sunset, and therefore before *A. dorsata* queens and drones are known to take their mating flights elsewhere in the range of the species (refer to details in the Introduction). The consistency with which *A. dorsata* drones take their mating flights just prior to and after sunset wherever the species has been studied makes it extremely likely that they also fly at dusk at our study site. Therefore, these two species are probably isolated reproductively by means of allochrony of mating where they co-occur in northern Vietnam, as was suggested by others may be the case in Nepal (McEvoy and Underwood 1988; Underwood 1990b; Koeniger and Koeniger 2000). Unfortunately, without direct observations of *A. dorsata* colonies at our study site, we are unable to confirm isolation by allochrony of mating.

In conclusion, our observations strongly suggest that *Apis laboriosa* is reproductively isolated from *Apis dorsata* by mating at different times of day. Furthermore, mating flights by *A. laboriosa* drones occur in Vietnam much later than in Nepal, providing another example of intraspecific differences in mating times of a honey bee species. Regional disparities in mating flight times (Otis et al. 2000), such as the difference in drone flight times of *A. laboriosa* between Nepal and Vietnam, limit their usefulness for inferring species status of honey bee populations to sites where taxa are sympatric.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-023-01014-y>.

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AUTHOR CONTRIBUTION

Hanh D. Pham and Gard W. Otis conceived this project and designed the methodology, with input from Chinh H. Phung. Hanh D. Pham, Dien T. Bui, and Thanh T. Nguyen conducted the field work. Dien T. Bui, Lam D. Nguyen, Chinh H. Phung, and Thanh T. Nguyen extracted data from videos. Karen J. Hand of Precision Strategic Solutions, Puslinch, Ontario, conducted the data analyses. Gard W. Otis and Hanh D. Pham wrote the manuscript that all authors reviewed and approved prior to it being submitted for publication.

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DATA AVAILABILITY

The data are included in the on-line supplementary material.

CODING AVAILABILITY

The coding used in statistical analyses is provided in the supplementary information.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

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Conflict of interest The authors declare no conflict of interest.

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