

CONGREGATIONS OF TEAR DRINKING BEES AT HUMAN EYES: FORAGING STRATEGIES FOR AN INVALUABLE RESOURCE BY *LISOTRIGONA* IN THAILAND (APIDAE, MELIPONINI)

*Hans Bänziger*¹

ABSTRACT

Wild *Lisotrigona cacciae* (Nurse) and *L. furva* Engel were studied in their natural forest habitat at three sites in northern Thailand, May 2013–November 2014. The author, both experimenter and tear source, marked the minute bees while they drank from his eyes viewed in a mirror. All marked workers, 34 *L. cacciae* and 23 *L. furva*, came repeatedly to engorge, 34 and 27 times on average, respectively. The maximum number of times the same *L. cacciae* and *L. furva* came was 78 and 144 visits in one day, respectively; the maximum over two days was 145 visits by one *L. cacciae*; the maximum number of visiting days by the same bee was four over seven days by one *L. furva* which made 65 visits totally. The same forager may collect tears for more than 10 h in a day, on average for 3 h 15 min and 2 h 14 min for *L. cacciae* and *L. furva*, respectively. Engorging from the inner eye corner averaged 3.1 and 2.2 min, respectively, but only 1.3 and 0.9 min when settled on the lower eye lid/ciliae. The interval between consecutive visits averaged 3.3 min and 3.8 min, respectively. Lachryphagy occurred during all months of the year, with 91–320 foragers a day during the hot season and 6–280 foragers during the rainy season; tear collecting resumed after a downpour. During the cold season eye visitation was reduced to 3–64 foragers, but none left her nest when the temperature was below 22° C. Flying ranges were greater than in comparable non-lachryphagous meliponines. It is proposed that *Lisotrigona* colonies have workers that are, besides nectar and pollen foragers, specialized tear collectors. Tears are 200 times richer in proteins than sweat, a secretion well-known to be imbibed by many meliponines. Digestion of proteins dissolved in tears is not hampered by an exine wall as in pollen, and they have bactericidal properties. These data corroborate the inference that *Lisotrigona*, which also visit other mammals, birds and reptiles, harvest lachrymation mainly for its content of proteins rather than only for salt and water.

Keywords: engorging time, flying range, lachryphagy, marking, round trip time, tear protein, visiting frequency

INTRODUCTION

Besides MICHENER's (2000) monumental work on the world's bees, the last couple of decades have seen fundamental advances in stingless bee research. For example, Nieh and colleagues' results on meliponine communication (NIEH & ROUBIK, 1995; NIEH *ET AL.*, 2003a, b; NIEH, 2004; NIEH *ET AL.*, 2005; CONTRERA *ET AL.*, 2007; SÁNCHEZ *ET AL.*, 2008), Biesmeijer and co-workers' findings on meliponine social foraging habits (e.g. BIESMEIJER *ET AL.*, 1998; BIESMEIJER & TÓTH, 1998; BIESMEIJER & DE VRIES, 2001; BIESMEIJER & SLAA, 2004; SLAA *ET AL.*,

¹ Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand. E-mail: hans.banziger@cmu.ac.th

Received 14 August 2017; accepted 6 January 2018.

2003), and Rasmussen's taxonomic and phylogenetic reassessment of the genera (RASMUSSEN & CAMERON, 2007, 2010; RASMUSSEN & CAMARGO, 2008). With previous extensive work (e.g. CAMARGO & PEDRO, 2003, 2004; ROUBIK, 1989, 2006), and a recent review (VIT *ET AL.*, 2013), meliponine research has thus been overwhelmingly Neotropical, reflecting that region's preponderance in stingless bee biodiversity. In Thailand, just over 30 species have been found (MICHENER & BOONGIRD, 2004; KLAKASIKORN *ET AL.*, 2005; THUMMAJITSAKUL *ET AL.*, 2008), but research has focused mainly on applied aspects (e.g. BOONGIRD, 2010; CHUTTONG *ET AL.*, 2016), faunistics and nest entrance types (e.g. RAJITPARINYA, 2001; INSON & MALAIPAN, 2006; BOONTOP *ET AL.*, 2008; BÄNZIGER *ET AL.*, 2011; KAMYOTCHAI *ET AL.*, 2015).

However, one feature about meliponines has not yet been documented from the Neotropics: lachryphagy (Figs. 1, 2). *Lisotrigona cacciae* (Nurse), *L. furva* Engel, and to a lesser extent *Pariotrigona klossi* (Schwarz), were found to suck persistently, in significant numbers, tears from human, other mammal, bird and reptile hosts in Thailand (BÄNZIGER *ET AL.*, 2009; BÄNZIGER & BÄNZIGER, 2010; BÄNZIGER *ET AL.*, 2011). Lachryphagy is exhibited pan-tropically by many nocturnal Lepidoptera (Geometridae, Pyralidae, Nolidae, Notodontidae, Thyatiridae [according to some authors a subfamily of Drepanidae], Sphingidae) (e.g. REID, 1954; BÜTTIKER & WHELLAN, 1966; BÜTTIKER, 1973; BÄNZIGER, 1973, 1988, 1995) and diurnal Diptera (Chloropidae, Cryptochetidae, Drosophilidae, Muscidae) (e.g. HALL & GERHARDT, 2002; MOON, 2002; OTRANTO *ET AL.*, 2005; MÁCA & OTRANTO, 2014). The lack of reports from the Neotropics on lachryphagous meliponines is surprising since recently the world's first two cases of a *Centris* bee (Apidae, Anthophorini) have been documented photographically while hovering in front of the eye of a turtle in Ecuador (DANGLES & CASAS, 2012) and a caiman in Costa Rica (DE LA ROSA, 2014).

Allied to lachryphagy is the more widespread sucking of sweat, exhibited not only by sweat bees (Halictidae) but also by many meliponines, including Afro- and Neotropical species, as well as by other bees (including *Apis cerana* F.) and many other insects (e.g. MICHENER, 1974, 2000; BARROWS, 1974; ROUBIK, 1989; BÄNZIGER *ET AL.*, 2009). *Lisotrigona* also imbibed sweat but to a much lesser extent than tears. Uptake of sweat and tears by various insect groups is generally interpreted as a means to obtain salt (NaCl). However, I had proposed that tear drinking meliponines primarily seek lachrymation for its high content of valuable proteins, which are in amounts on a par with salt (see Discussion).

The present study addresses the following questions: (1) Does a *Lisotrigona* forager suck tears to satiate her own individual needs or does she harvest tears for her nest's social requirements, returning repeatedly to collect more? (2) If the latter applies, how many times and for how many hours during that and subsequent days does a particular worker return to a human host, for how long does she imbibe tears each time, and how long are intervals between visits? (3) Are tears harvested continuously for days, weeks, one season, or year-round? (4) How many foragers engage in lachryphagy each month, when do they first arrive in the day, reach maximum numbers, and when do they stop foraging? (5) What is the lowest temperature and earliest time when *Lisotrigona* leave their nest? (6) What is *Lisotrigona*'s flight range?

MATERIALS AND METHODS

The study was carried out on wild bees in their natural habitats. This should dispel possible criticism that tear drinking is an abnormal behavior, and the results artifacts due, e.g.

to the use of bees in hives in an unnatural environment. Research was carried out alone to avoid bees becoming confused and misled by more than one human source. Also, while the potential for eye disease contraction (cf. BÄNZIGER *ET AL.*, 2009) appears to be low (but note the recent detection of the Zika virus in tears [MINER *ET AL.*, 2016]), I felt that the risks involved were to be solely my own.

Study sites were all in Chiang Mai Province, northern Thailand: site A, a forest spot south of Chang Khian stream, 650 m a.s.l.; site B, south of Pha Lad stream, similar elevation, but about 3 km to the south of site A, both on Mount Suthep; and site C, at the foot of a limestone rock face, Chaiprakan, 780 m a.s.l., just over 100 km N of site A. The habitats were dominated by primary mixed deciduous forest. A steep hike of over one hour was required to reach site A. However, at site A the forest was relatively open, so that many and wide sunflecks reached the ground, while at site B it was denser, with thicker undergrowth and more closed canopy, hence clearly darker especially as the rainy season progressed. Site C was also relatively open but dominated by bamboo, with fewer tree species though a more diverse forb layer. At site A a perennial stream was 200 m from the study spot, at site B there were streams and pools with perennial water 20–100 m away, at site C I offered water in a basin (25 cm diameter) during the dry season 5–10 m from the study spot.

Both *L. cacciae* and *L. furva* occurred at the three research sites, but at site A there were nearly exclusively *L. cacciae*, at B *L. furva* was slightly more numerous, and at C there were overwhelmingly *L. furva*. Unfortunately, I have been unable to find any *Lisotrigona* nests at these sites despite repeated search over the years. Elsewhere I found them hidden in hollows of tree trunks or limestone rock faces and the only indication of their presence was an entrance hole just 1.5–7 mm across, often at the end of an inconspicuous tubelet (BÄNZIGER *ET AL.*, 2011). I chose not to use these nest sites for the present study for two reasons: they were not in fully natural habitats (near roads, at a wide clearing for cars, human constructs, or fruit orchards), and *Lisotrigona*'s lachryphagous habits were irregular there. However, in order to answer question (5), not possible without a nest, I used a nest of *L. furva* in a semi-natural habitat, a garden dominated by fruit trees, ornamentals and exotics in a suburb of Chiang Mai town (site D).

The field study period was May 2013 to November 2014. There are three seasons in northern Thailand which are best characterized as cool-dry (cold season, mid-November–mid-February), hot-dry (hot season, mid-February–April), and hot-wet (rainy season, May–mid-November). Temperature and humidity were registered with a portable digital thermohygrometer (Dostmann, P330, resolution 0.1° C, 0.1% rH).

Identification of *L. cacciae* and *L. furva* workers followed ENGEL (2000), the improved treatment by MICHENER (2007) and new data by BÄNZIGER & BÄNZIGER (2010). The identification of *Tetragonula hirashimai* (Sakagami), *T. testaceitarsis* (Cameron), *T. fuscobalteata* (Cameron) and *T. laeviceps* (Smith) was based on SAKAGAMI (1978) and RASMUSSEN & MICHENER (2010). However, it is evident that each of these taxa consists of cryptic species (BÄNZIGER, unpublished) at present still under investigation. Because intermediates occur, *T. hirashimai* and *T. testaceitarsis* could not yet be clearly separated in the studied population; for simplicity I am using *T. hirashimai*. *Tetrigona apicalis* (Smith) was identified using SCHWARZ (1939). Generic abbreviations used in the text: *Lisotrigona* (*L.*), *Tetragonula* (*T.*), *Tetrigona* (*Tetri.*), *Trigona* (*Tri.*).

To avoid repetitions, only data additional to, or different from, those already published (BÄNZIGER *ET AL.*, 2009, BÄNZIGER & BÄNZIGER, 2010) are mentioned.

All photographs are by the author.

Experimental Set-up

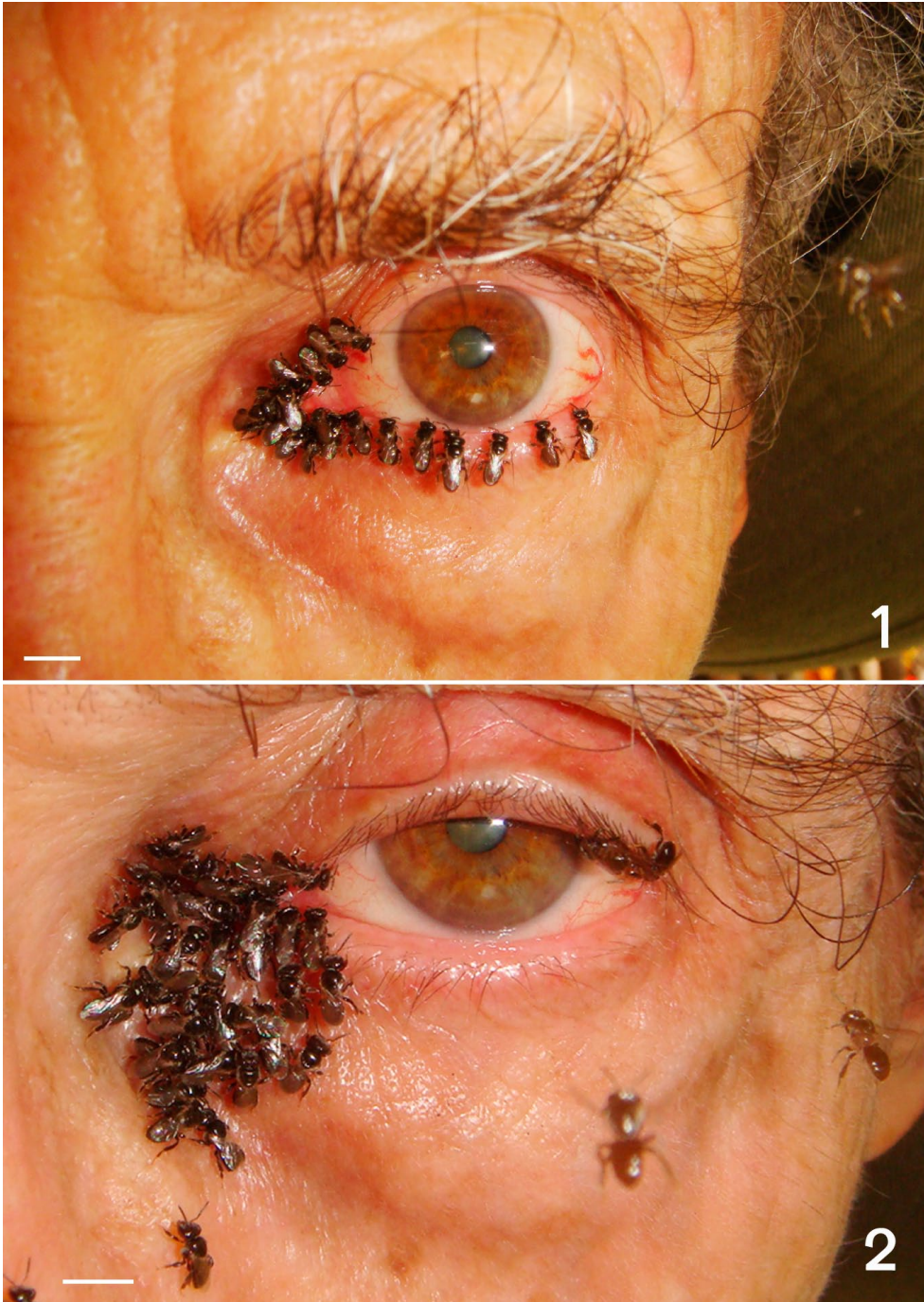
To answer questions (1)–(3) and (6), bees were individually marked. Captured *Lisotrigona* were too restless for applying paint or tags, unlike when they avidly imbibed my tears. However, marking Asia's smallest bees (*L. cacciae*: head width 1.05–1.23 mm, wing length (including tegulae) 2.6–2.8 mm, body length (metasoma dry, more or less telescoped) 2.3–3.0 mm) in the field while they were sucking at my eyes worked only in one of 2–4 attempts. The markable area was the dorsum of the thorax 0.8×0.9 mm in *L. cacciae* and 1.0×1.1 mm in *L. furva*. A minuscule drop of waterproof paint (white, dark yellow, green, or red) was applied with the finest available brush, additionally trimmed. This was introduced between my eyeglasses and eyebrows with my right hand, the left one holding a small electric torch to illuminate the process, viewed in a concave mirror. Occasionally the paint inadvertently extended to the occiput but it did not handicap the bee since she continued to come (but the dot on the head was often removed overnight in the nest; cf. Figs. 3–4, 6–7). Usually only one or two bees were marked during one day. The follow-up of more than two marked bees was difficult when many others were sucking at the same time or continuously arriving and leaving. Shape, position and color of the mark on each bee were recorded photographically for accurate identification of that bee, potentially over several days.

For questions (1) and (2) each arrival time, duration of sucking, and leaving time of the marked bee were noted, including her position and behavior at the eye, from the time of her marking, including all subsequent returns, until her last visit. The latter was assumed to be the case when she failed to return for at least 15 min (min/max return trip time was 1.5–8.0 min).

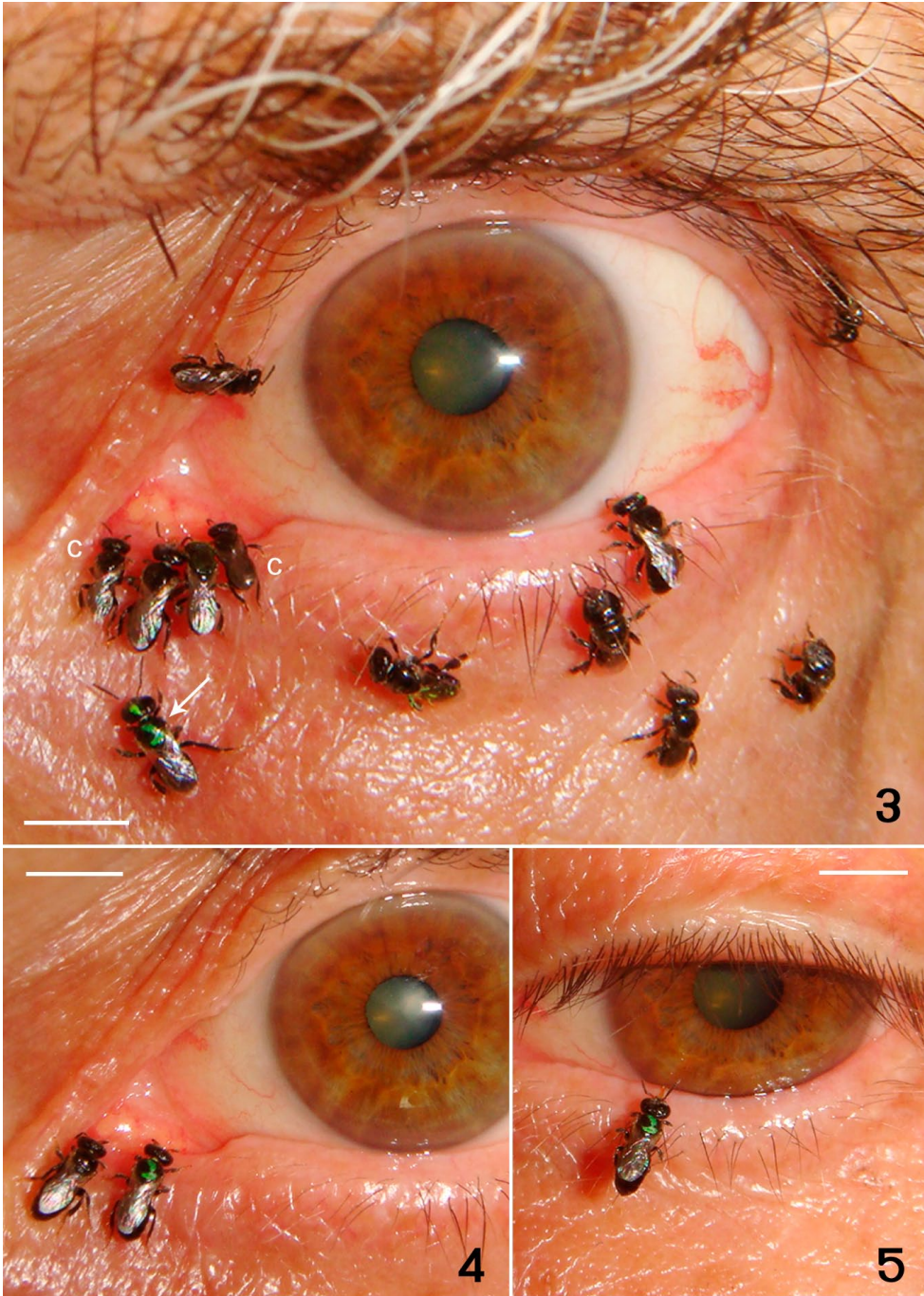
To investigate question (3), whether *Lisotrigona*'s tear requirement was brief (a few hours/days) or long-term (several weeks), I presented myself to the bees during 21 consecutive days at site B, 31 May to 20 June, 2013. For the assessment of whether the requirement was seasonal or continuous (year round), I presented myself at least once a month, May 2013–November 2014, at sites A and C. Observation time had to be adjusted to weather conditions. Also, some days the bees were too pestiferous to bear them for more than a couple of hours, so that the observations had to be discontinued as soon as the relevant data had been obtained.

To assess the number of visiting bees (question 4), two methods were used, a) when bees were not too numerous, b) when many bees were involved. For a), a film canister was placed over the eye until the bee(s) flew into the canister which was then rapidly closed. At the end of the day's study the bees were counted and released. Method b) was used when bees were so numerous that not all could find space at my eyes but continuously flew around my head, attempted to land, fell off, and resumed circling my head. They were caught by net at 10–20-min intervals. This method was less exact as many managed to escape the net or when transferred to cylindrical plastic boxes (height 10 cm, diameter 9 cm). At the end of the study they were slightly narcotized with ethyl acetate, counted and released.

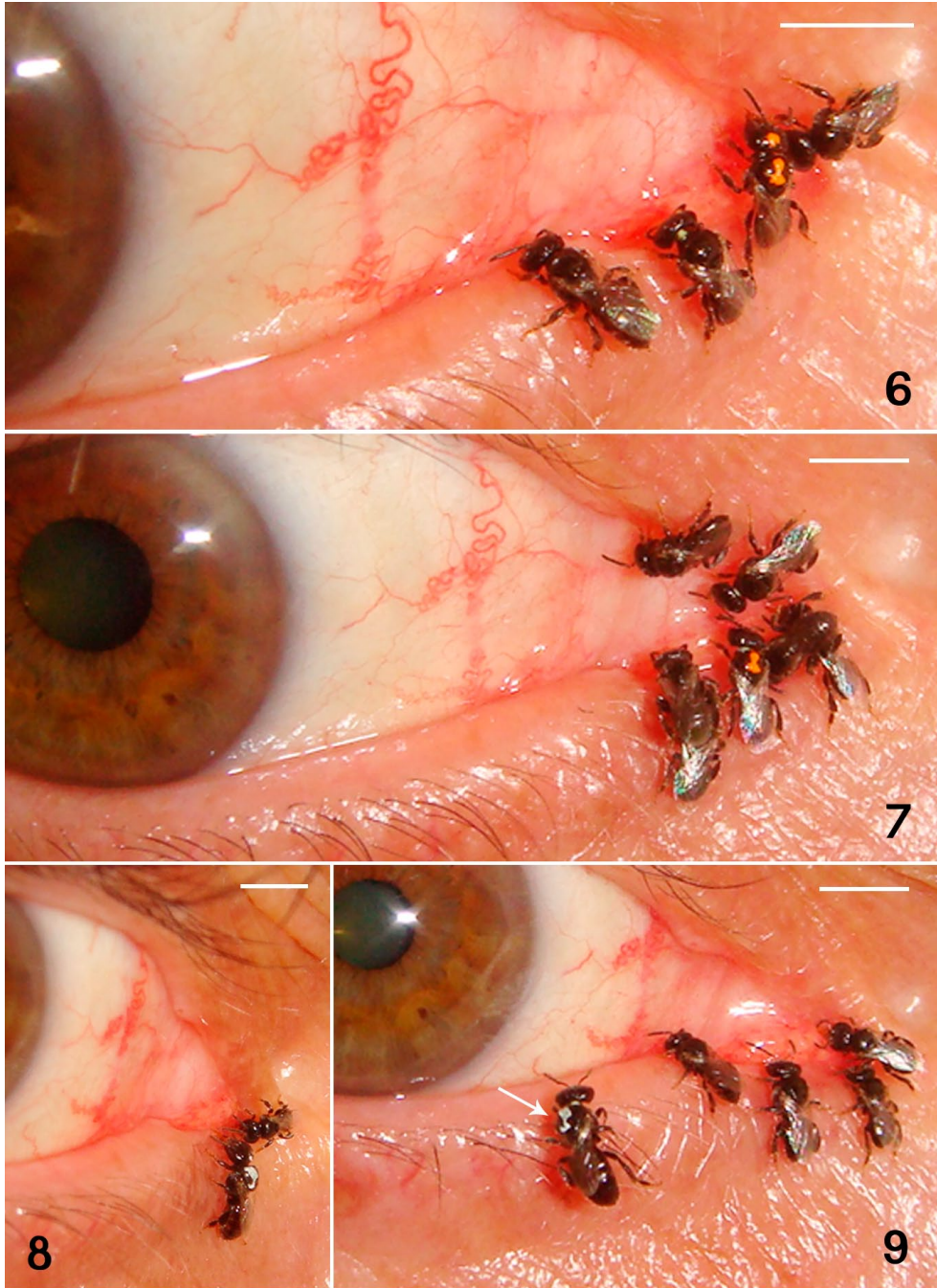
For question (5), the lowest nest-leaving temperature was measured during the coldest period (December–January) whereas the earliest nest-leaving time was assessed when days were longest and generally warmest in early morning (June–July). The sensor of a digital thermometer (Ebro, TFX 430, resolution 0.02° C) was placed in constant shade 5 cm from the entrance of the nest of *L. furva* at site D. On observation days the nest entrance was kept under constant watch starting one hour prior to the expected beginning of the foraging. The watching spot was 4 m diagonally from the nest entrance, so that part of a forager was visible by binocular (8×32) while still inside the entrance tube, a few mm from its rim. For compari-



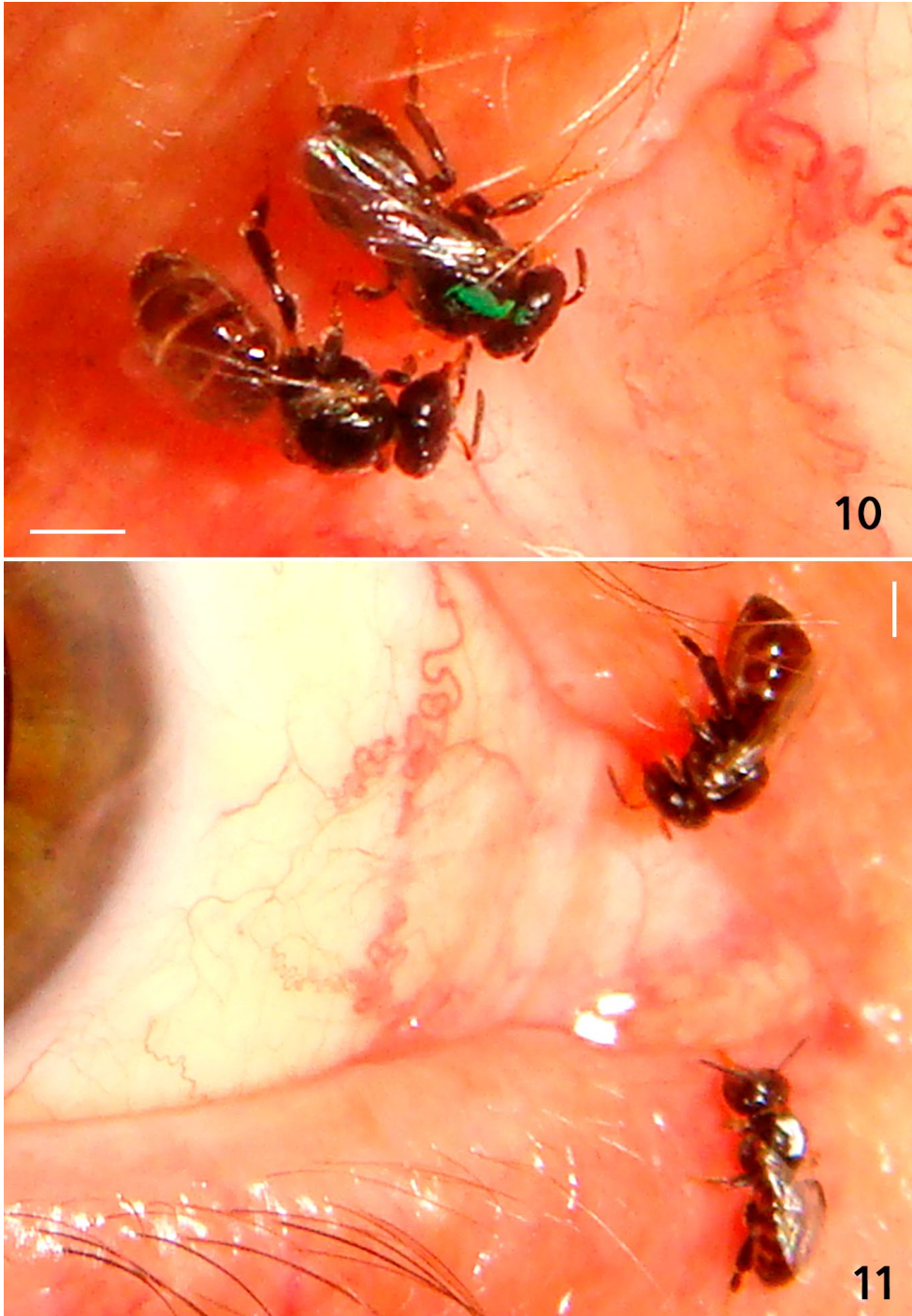
Figures 1–2. Lachryphagous *Lisotrigona*. (1) Row of 20 *L. furva* sipping author’s tears. (2) Largest congregation of *L. furva*: 31–33 at the eye or below where tears flowed down, two at the upper eyelid, several out of frame. The bees were endured just long enough for this photo. Bars = 4 mm. All self-portraits by the author.



Figures 3–5. Green marked *Lisotrigona furva* (L.f.3, arrow) came consecutively on three days and once more on the 7th, a total of 65 times in 4 days. (3) Day 1, 2nd visit. (4) Day 2, 12th visit; day 3 not shown. (5) Day 7, 1st visit. Bars = 4 mm, c = *L. cacciae*.



Figures 6–9. Consecutive day visits by *Lisotrigona*. (6) Red marked *L. cacciae* (L.c.24) on the 8th of her 68 visits on day 1, 24.ii.2014. (7) L.c.24 on the 21st of her 74 visits on day 2, 25.ii.2014, (8) White marked *L. furva* (L.f.1) on the 58th of her 72 visits, day 1, 31.v.2013. (9) L.f.1 (arrow) on the 10th of her 12 visits on day 2, 1.vi.2013, with 4 unmarked *L. cacciae*, Bars = 3 mm.



Figures 10–11. Tear-turgid crop in distended abdomen of *Lisotrigona*. (10) Unmarked *L. cacciae* below green marked L.c.10, site A, 14.viii.2013. (11) Unmarked *L. furva* above white marked L.c.4, site B, 7.vi.2013. Bars = 1 mm.

son of the lowest nest-leaving temperature with other species, *T. laeviceps* and *Tetri. apicalis*, were checked, three nests each, on six occasions in the campus of Chiang Mai University during the cold season. For comparison of the earliest nest-leaving time, the first arrival of *T. hirashimai* at spider lilies (*Hymenocallis caribaea* [L.] Herb.) at site D was noted. Her nest's location was not known, hence her earliest arrival time at the flowers was used as a conservative estimate of the earliest nest-leaving time.

To assess the foraging and homing range of *Lisotrigona* (question 6) my approach was different from conventional methods because the location of the nest was not known, but I took advantage of the fact that the tear source is naturally mobile, unlike flowers. The first of my two methods assessed the foraging range (as in LINDAUER [1956]), whereas the second assessed the homing range (as in ROUBIK & ALUJA [1983], and GOULSON & STOUT [2001]). Both of my methods allowed for two values in each experiment, viz. a potential high and an absolute lowest. For the high value, the nest's location was assumed to be at 20–50 m from the study site (see Results); for the absolute lowest value the nest was assumed to be half way between the start and the end of each experiment (the shortest possible distance from nest to both the start and the end). The first method was based on the habit of *Lisotrigona* to pursue a slow-moving host. I walked slowly (about 2 km/h) away from the study site with several *L. furva* circling around my head attempting to land at my eyes, until where the last bee discontinued pursuit (on 15.x.2013, $n = 4$). The second method was based on *Lisotrigona*'s "riding-while-drinking" habits. I ran "resiliently" (i.e. minimizing the shock of the soles against the ground, about 5–8 km/h), with a marked tear drinker riding my eye, on 30.i., 10.ii., 24.iii., and 21.v.2014. I noted where and when she landed, where and when she flew off, and if and when she returned for more once I was back to the study site. If she did return, it meant that she (a) was able to fly and orient herself over this distance to first deliver my tears to her nest and then (b) return to my eye. This experiment was done five times with five different bees (L.f.21, L.f.22, L.f.28, L.f.29, L.f.36) in the same direction as in the first method but two times in the opposite one. For the latter, two bees were selected among the five which had been successful in returning from the previous direction (L.f.21, L.f.29). Unfortunately, the terrain in the opposite direction was steep uphill, reducing my speed to about half. In all 11 trials the distance covered was marked on the ground and measured at the end of the day by the number of my strides of 0.75 m. Greater distances could not be assessed both because the maximum tear drinking duration was mostly around 6 minutes, and because I was unable to run faster without shaking my body.

RESULTS

Observations on Approach, Landing and Feeding Behavior of *Lisotrigona* at Eyes

The typical zig-zag flying of the initially inexperienced forager on approaching the eye was reduced as she became increasingly familiar with a particular host/eye: she arrived in a relatively straight flight, slowed down and landed on the ciliae of the lower eyelid, or less often on adjacent skin around the eye from where she crawled to the eyeball. Occasionally the landing was so gentle that I did not or just barely noticed it. There are four vantage spots from where she extended her proboscis (well visible in Fig. 5) into the tear trough between eyelid and eyeball: the inner and outer eye corner, the lower and upper eyelid (with front legs resting on the conjunctiva, the other legs on the ciliae). Sucking from the outer eye corner

and upper eyelid were much less frequent. In order not to topple from the upper eye lid, the forager had to firmly claw the lid, causing appreciable discomfort. I could not refrain from repeatedly blinking the lid and in most cases I eventually had to dislodge the tormentor from this position. Once the bee stopped crawling and started sucking, generally I felt rather little or no discomfort; on occasions I had to check by mirror whether she was still there or not. While sucking, the antennae might repeatedly touch the substrate and then be groomed. At times a burning sensation was felt. As the sucking progressed, the metasoma was clearly seen distending remarkably in length to 1.9 mm in *L. cacciae* and 2.3 mm in *L. furva* when fully engorged (dry telescoped state 0.68–1.03 mm and 0.9–1.4 mm, respectively), as well as in width, exposing the translucent membranes between tergal and sternal plates of each segment (Figs. 10, 11). In many cases a slight tickling was felt at the feeding site after she had left. This tickling became a prurigo after more and more bees had been sucking, so that at times I could not restrain myself from vigorously rubbing my eyelid, after having gently dislodged any persisting guest. Neither inter- nor intraspecific antagonistic behavior was noted among congregated tear drinkers (Figs. 3, 9), even when sucking in a dense, mixed-species cluster. However, some shoving aside, or landing on the back of already sucking bees, occurred in such cases, often without the rider being dislodged (Figs. 1, 7). The presence of several bees felt tickly, and crowded congregations could be unpleasant to unbearably irritating, in which case I collected the bees for counting and release at the end of the session. I interpret this tickling as mainly mechanically-induced unlike the previous instance which may have been chemically-based. A couple of times pinching of the lid occurred.

Marking and other Experiments

Questions (1) and (2): All 57 marked *Lisotrigona*, 34 *L. cacciae* and 23 *L. furva*, returned to my eyes repeatedly to collect tears, but one *L. cacciae* and one *L. furva* made only two trips each (Tables 1–3). The maximum number of trips in one day was 78 in *L. cacciae* and 144 in *L. furva*, the averages were 34 ($n = 37$) and 27 ($n = 15$) times, respectively (note that the values for n do not correspond to the values given above because some bees came also on subsequent days, whereas others were not considered because used for experiments on foraging range, or observations were cut short as bees were too pestiferous). Of 12 *L. cacciae* and 6 *L. furva* for which data are available on consecutive day observations, five *L. cacciae* (41.7%) and five *L. furva* (83%), resumed tear drinking the following day (Figs. 6–9). *Lisotrigona furva* L.f.3 was special in coming for four days, consecutively on three and once again four days later (Figs. 3–5). The overall maximum for one collector was 145 trips in two days by L.c.40. The much higher number of consecutive-day returnees in *L. furva* probably is coincidental; fewer *L. cacciae* were available for such observations (Table 3).

Table 4 lists the duration of sucking and of round trips (i.e. interval between flying off the eye to the nest, disgorging the tears, and arrival back at the eye) of 4 *L. cacciae* and 4 *L. furva* selected from the most complete data. The first two sucking durations and round trip durations of the 8 bees were not considered because they tended to be irregular as the bee had not yet adjusted to the newly found source and the fastest route to it. Also discarded were the occasional unusually long or short sucking and round trip, when she possibly took a rest or, after flying off the eye due to feeding disruption (e.g. by dense crowding) she did not return to the nest unsatiated but presumably remained in the vicinity. In *L. cacciae* a single tear drinking bout lasted 0.4–3.0 min, average 1.3 min ($n = 64$) when settled on the lower eye lid/

Table 1. Time and number of return trips by marked *Lisotrigona cacciae* sucking human tears, and total number of workers involved, every month January–December, site A. Listing not in chronological order of field studies. No marking on 5.xi.2014 when no *Lisotrigona* arrived on a rainy day. RH = relative humidity; T = temperature in °C, minimum refers to when the first bee arrived, not when study started; a third T reading is given when T in the evening was lower than in the morning. †Time when paint applied or when the marked bee returned on the following day.

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked†	Number of trips	Time of last trip	Remarks
28.i.2014 1020–1750 h	1225 h 55	L.c.20	1312 h	54	1727 h	Low temperature and approaching dusk evidently induced L.c.20 to discontinue foraging. T: 23.9–25.2–21.5°, RH: 51–70%
24.ii.2014 1033–1735 h	1040 h 91	L.c.24 1 st day	1124 h	68	1629 h	L.c.24 absence for 1 h indicates that she stopped foraging after 68 trips. She returned following day. T: 25.7–30.5°, RH: 36–52%
25.ii.2014 0943–1750 h	0950 h 96	L.c.24 2 nd day	Returned 1056 h	74	1714 h	Approaching dusk possibly induced L.c.24 to stop foraging after 74 trips (142 in 2 days) T: 26.7–30.8°, RH: 33–49%
27.iii.2014 1007–1509 h	1012 h about 300	L.c.30	1034 h	26	1347 h	L.c.30 absence for 1h indicates that she stopped foraging after 26 trips. Study discontinued early, bees too pestiferous. T: 28.3–34.5°, RH: 25–47%
28.iv.2014 0847–1550 h	0854 h about 160	L.c.34	0935 h	13	1035 h	L.c.34 absence for 5 h indicates that she stopped foraging after 13 trips. Study discontinued early, bees too pestiferous. T: 27.7–35.7°, RH: 39–67%
25.v.2014 0817–1315 h	0826 h about 190	L.c.35 L.c.37	1033 h 0940 h	55 2	1455 h 0948 h	L.c.35 absence for 55 min indicates that she stopped foraging after 55 trips L.c.37 absence for 3 h indicates she stopped foraging after 2 trips. Study discontinued early, bees too pestiferous. T: 27.7–33.5°, RH: 56–77%
		L.c.38 L.c.39	1002 h 1119 h	5 6	1033 h 1156 h	L.c.38 absence for 2.5 h indicates she stopped foraging after 5 trips L.c.39 absence for 2 h indicates she stopped foraging after 6 trips. T: 27.7–33.5°, RH: 56–77%

Table 1 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
20.vi.2014 0711–1903 h	0806 h 88	L.c.40 1 st day	0949 h	67	1818 h	L.c.40 resumed foraging after strong rain of 1434–1450 h; approaching dusk evidently induced her to stop foraging. Returned the following day. T: 25.4–30.0°, RH: 72–99%
		L.c.41	1205 h	30	1435 h	L.c.41 absence for 4 h indicates she stopped foraging after 30 trips. Did not return the following day
		L.c.42	1548 h	44	1847 h	Approaching dusk evidently induced L.c.42 to stop foraging after 44 trips. Did not return the following day
21.vi.2014 0746–1852 h	0755 h 74	L.c.40 2 nd day	Returned 0755 h	78	1822 h	Approaching dusk evidently induced L.c.40 to discontinue foraging after 78 trips (145 in 2 days). T: 25.0–28.4°, RH: 93–99%
17.vii.2014 0656–1830 h	1020 h 101	L.c.45 1 st day	1108 h	64	1805 h	Rain drizzle 1403–1436 h reduced but not stopped foraging by L.c.45; no foraging in strong rain 1455–1540 h; foraging resumed 12 min after rain stopped; foraging discontinued after 64 trips as dusk approached. Returned the following day. T: 29.2–34.5°, RH: 82–99%
		L.c.46 1 st day	1606 h	21	1808 h	Approaching dusk probably induced L.c.46 to discontinue foraging after 21 trips. Returned the following day
18.vii.2014 0959–1800 h	1009 h 59	L.c.45 2 nd day	Returned 1009 h	54	1529 h	L.c.45 continued foraging during rain drizzle 1334–1338 h; discontinued during strong rain 1457–1510 h; resumed 1515–1525 h during drizzle; discontinued after 54 trips (118 in two days) as strong rain approached 1538–1600 h followed by drizzle with low temperature and dark clouds until dusk. T: 26.2–27.3–23.1°C, RH: 80–99%
		L.c.46 2 nd day	Returned 1024 h	54	1526 h	Same inclement weather as for L.c.45, 2 nd day. Foraging stopped after 54 trips (75 in two days)

Table 1 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
13.viii.2014 0806–1710 h	1039 h 18	L.c.49	1115 h	21	1221 h	Rain drizzle 3 times early afternoon possible cause for L.c. 49 not to return after 21 trips; dark clouds and strong rain from 1710 h until dusk. T: 25.9–26.9°, RH: 80–99%
		L.c.50	1253 h	11	1353 h	L.c.50 returned after rain drizzle but only 3 times; inclement weather from 1710 h until dusk
		L.c.51	1511 h	41	1648 h	Inclement weather evidently caused L.c.51 to stop foraging after 41 trips
14.viii.2013 1053–1800 h	1106 h 23	L.c.9	1157 h	40	1740 h	L.c.9 abnormal, slow and irregular forager; approaching rain 1746 h evidently caused L.c.9 to discontinue foraging after 40 trips. T: 27.4–30.0°, RH: 74–99%
		L.c.10	1347 h	18	1519 h	L.c.10 absence for 2.5 h indicates she stopped foraging after 18 trips
8.ix.2014 0824–1754 h	1049 h 83	L.c.52	1115 h	8	1152 h	Absence for 37 min indicates L.c.52 stopped foraging possibly due to disturbance by many foragers. T: 27.9–28.6°C, RH: 79–90%
		L.c.53	1116 h	9	1157 h	Absence for 6 h indicates L.c.53 stopped foraging after 9 trips, possibly due to disturbance by many foragers
		L.c.54	1319 h	35	1715 h	Absence for 40 min indicates L.c.54 stopped foraging after 35 trips
23.ix.2013 1028–1825 h	1233 h 9	L.c.14	1444 h	35	1806 h	Approaching dusk evidently induced L.c.14 to stop foraging after 35 trips. T: 25.8–30.2°, RH: 66–93%
4.x.2014 0757–1723 h	1019 h 84	L.c.55	1042 h	76	1519 h	Absence for more than 2 h indicates she stopped foraging after 76 trips. T: 27.7–30.4°, RH: 60–84%
10.x.2013 1007–1805 h	1259 h 6	L.c.15	1452 h	39	1735 h	Approaching dusk evidently induced L.c.15 to stop foraging after 39 trips. T: 23.8–28.0°, RH: 66–93%

Table 1 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
9.xi.2014 0856–1756 h	1053 h 57	L.c.56 L.c.57	1128 h 1454 h	56 31	1734 h 1730 h	Approaching dusk evidently induced L.c.56 to stop foraging after 56 trips. T: 24.8–28.3–24.2°, RH: 81–93% Approaching dusk evidently induced L.c.57 to stop foraging after 31 trips
7.xii.2013 1043–1717 h	1151 h 3	L.c.18	1256 h	8	1353 h	L.c.18 absence for 3 h indicates that she stopped foraging after 8 trips, probably due to low temperature, which also reason for few bees. T: 22.7–23.5–21.1°, RH: 61–83%
		L.c.19	1326 h	25	1622 h	L.c.19 absence for 55 min indicates that she stopped foraging after 25 trips, evidently due to low temperature

Additional cases of *L. cacciae* but from site B (not mentioned in Table 3 because not part of the 21 consecutive days of observations).

L.c.25: marked 1237 h on 20.iii.2014, made 19 trips until 1405 h, did not return on 21.iii.2014.

L.c.26: marked 1520 h on 20.iii.2014, made 13 trips until 1634 h, returned on 21.iii.2014 at 1226 h, made 49 trips until 1542 h.

L.c.32: marked 1328 h on 17.iv.2014, made 13 trips until 1522 h, did not return on 18.iv.2014.

Table 2. Time and number of return trips by marked *Lisotrigona furva* sucking human tears, and total number of workers involved, every month January–December, site C. Listing not in chronological order of field studies. RH = relative humidity; T = temperature in °C, minimum refers to when the first bee arrived, not when study started; a third T reading is given when T in the evening was lower than in the morning. †Experiments for assessing the foraging/homing range, see text question 6.

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked	Number of trips	Time of last trip	Remarks
30.i.2014 1150–1810 h	1200 h about 420	L.f.21	1212 h	21	1700 h	L.f.21 used in experiments [†] 1330–1630 h, hence relatively few return trips. T: 23.5–28.6°C, RH: 36–56%. Unseasonally hot and dry, abnormally many bees
10.ii.2014 1045–1645 h	1050 h about 250	L.f.22	1057 h	7	1233 h	L.f.22 did not return after her 7 th trip in experiments [†] . Weather as above, many bees. T: 26.6–29.4°, RH: 30–40%
		L.f.23	1111 h	6	1220 h	Disturbance by dense crowding possible reason for few return trips by L.f.23. T: 26.6–29.4°, RH: 30–40%
24.iii.2014 1112–1805 h	1118 h about 220	L.f.27	1147 h	6	1228 h	L.f.27 exhibited rather irregular and pestiferous behavior, was captured after 6 trips. T: 23.6–29.2–21.3°, RH: 44–65%
		L.f.28	1234 h	7	1331 h	L.f.28 did not return after her 7 th trip in experiments [†]
		L.f.29	1430 h	14	1727 h	L.f.29 used in experiments [†] 1457–1701 h; later unusually low temperature caused her to stop foraging
22.iv.2014 1150–1350 h	1152 h about 320	L.f.33	1245 h	4	1303 h	Disturbance by dense crowding possible reason for few return trips by L.f.33; dozens of very pestiferous bees required early termination of observations
21.v.2014 1100–1510 h	1110 h about 220	L.f.36	1133 h	12	1406.5 h	L.f.36 used experiments [†] 1234–1336 h, hence relatively few return trips. T: 27.9–32.8°, RH: 51–68%
26.vi.2014 0626–1740 h	0748 h about 280	L.f.43	0818 h	103	1333 h	L.f.43 absence for 4 h indicates that she stopped foraging after 103 trips. T: 24.1–26.9°, RH: 81–99%
		L.f.44	1456 h	11	1613 h	L.f.44 absence for 1.5 h indicates that she stopped foraging after 11 trips

Table 2 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked	Number of trips	Time of last trip	Remarks
23.vii.2014 1148–1744 h	1207 h over 280	L.f.47	1313 h	7	1337 h	Disturbance by dense crowding possible reason for 7 trips only by L.f.47. T: 23.6–25.3–21.7°, RH: 95–99%
		L.f.48	1402 h	14	1513 h	L.f.48 stopped foraging due to strong rain 1516–1530 h followed by drizzle and canopy rain until 1645 h; did not resume foraging evidently due to low temperature and dark clouds
26.viii.2013 1105–1640 h	1118 h over 100	L.f.11	1137 h	4	1217 h	Bees very pestiferous, observations interrupted 1220–1520 h, L.f.11 did not return. Thermohygrometer non-functional
15.ix.2013 1034–1610 h	1100 h about 130	L.f.12	1117 h	19	1300 h	Approaching rain induced L.f.12 to discontinue foraging, did not return after rain stopped 1450 h, but 2 unmarked bees resumed lachryphagy 1545 h during canopy rain. T: 25.1–27.1°, RH: 88–99%
15.x.2013 1057–1645 h	1106 h over 200	L.f.16	1118 h	2	1123 h	Observations interrupted 1255–1530 h due to very pestiferous bees and for experiments'. T: 27.9–29.2°, RH: 68–73%
18.xi.2014 1039–1745 h	1214 h 64	L.f.58	1237 h	144	1726 h	Approaching dusk evident reason for L.f.58 to discontinue foraging. T: 24.3–26.2°, RH: 70–77%
4.xii.2013 1108–1705 h	1237 h 3	L.f.17	1319 h	24	1542 h	Low temperature evident cause for foraging termination by L.f.17, and presence of few bees. T: 25.7–21.3°, RH: 61–81%

Additional case of *L. furva* but from site B (not mentioned in Table 3 because not part of the 21 consecutive days of observations). L.f.31: marked 1310 h on 17.iv.2014, made 48 trips until 1749 h; returned 18.iv.14 at 1046 h, made only 2 trips until 1050 h.

Table 3. Twenty-one consecutive days of observations on *Lisotrigona* foraging for human tears. Number of *Lisotrigona cacciae* (Lc) and *L. furva* (Lf) involved and, when marked, time and number of return trips, site B, 31 May–20 June, 2013. RH = relative humidity; T = temperature in °C. ¹Time when paint applied or when the marked bee returned on the following days. N.B. the observations were mainly for checking whether tear collecting occurred daily over a longer period, hence bees were not always marked and observations often discontinued upon obtaining the relevant data.

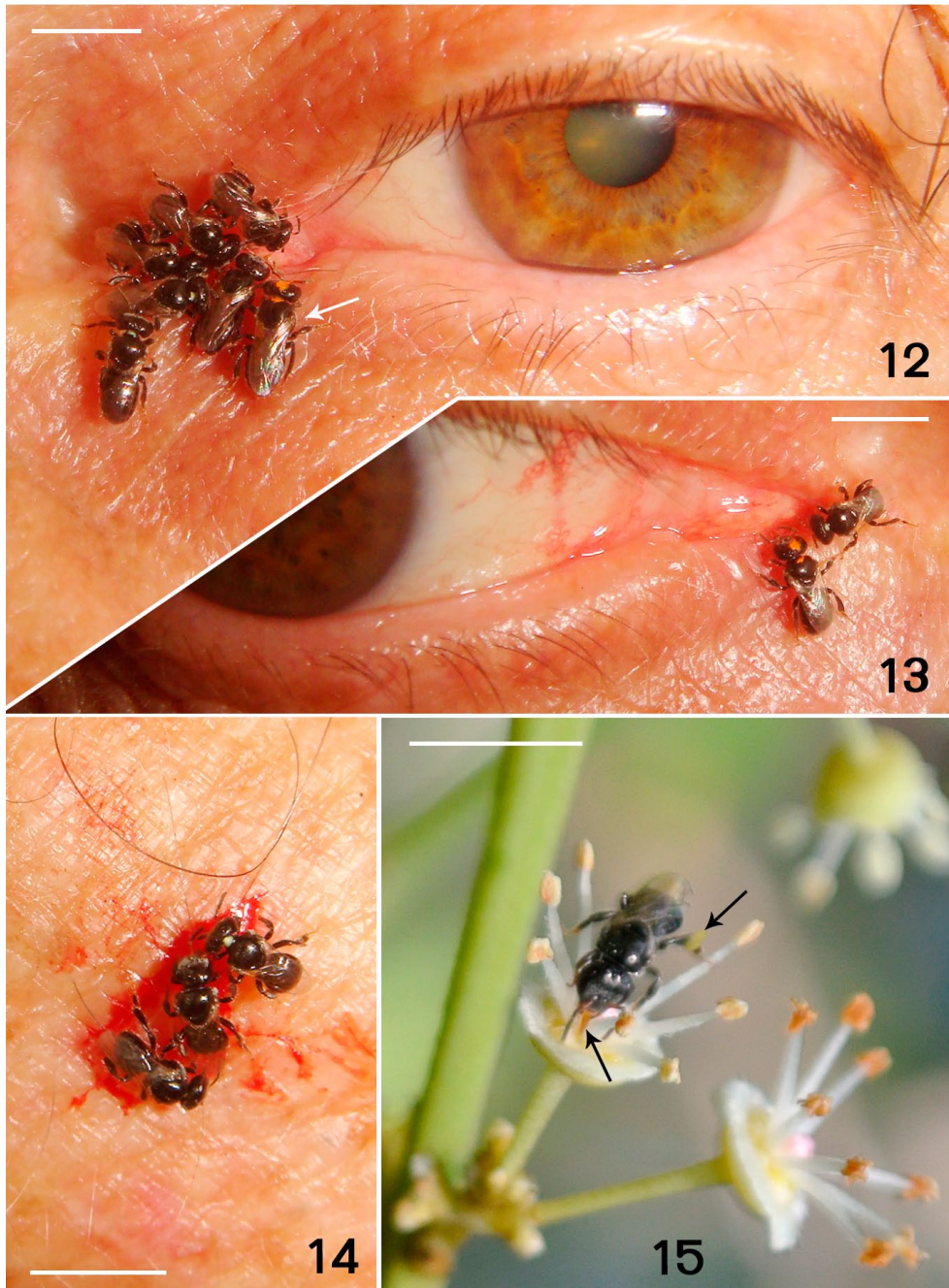
Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
31.v.2013 1030–1850 h	1148 h 5 Lc, 2 Lf	L.f.1 first day	1246 h	72	1824 h	Approaching dusk evidently induced L.f.1 to stop foraging after 72 trips, but resumed next day. T: 29.1–31.4°, 52–78%
1.vi.2013 1045–1316 h	1055 h 4 Lc, 5 Lf	L.f.1 second day	returned 1218 h	12	1315 h	L.f.1 might have continued foraging after 12 trips (84 in 2 days) but observations were terminated before. T: 28.7–31.2°, RH: 56–67%
2.vi.2013 1130–1540 h	1138 h 14 Lc, 15 Lf	None marked	-	-	-	Bees still foraging when observations terminated. T: 29.2–31.4°, RH: 55–67%
3.vi.2013 1134–1355 h	1140 h over 20, not identified	L.c.2	1205 h	15	1320 h	L.c.2 absence for 35 min after 1320 h indicates that she stopped foraging after 15 trips. Bees too pestiferous, study terminated early. T: 31.6–32.0°, RH: 55–60%
4.vi.2013 1117–1500 h	1125 h 10 Lc, 13 Lf	L.f.3 first day	1250 h	5	1447 h	L.f.3 flew few and irregular trips but resumed next day. T: 25.8–27.8°, RH: 75–87%
5.vi.2013 1125–1640 h	1130 h 4 Lc, 4 Lf	L.f.3 second day	returned 1215 h	18	1354 h	Rain induced L.f.3 to discontinue foraging after 18 trips; no bee returned after rain stopped 1505 h; L.f.3 resumed trips next day. T: 24.6–27.6°, RH: 78–99%
6.vi.2013 1207–1518 h	1212 h 5 Lc, 5 Lf	L.f.3 third day	returned 1236 h	29	1515 h	L.f.3 might have continued foraging for more than 29 trips but bees too pestiferous, study terminated early; no trips by L.f.3 the following 3 days but resumed 4 days later. T: 26.2–28.6°, RH: 73–85%
7.vi.2013 1252–1533 h	1259 h 4 Lc, 7 Lf	L.c.4	1346 h	23	1526 h	L.c.4 might have continued foraging for more than 23 trips but observations terminated before. T: 28.1–28.5°, RH: 69–82%

Table 3 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
8.vi.2013 1336–1552 h	1347 h 3 Lc, 5 Lf	L.f.5 first day	1503 h	15	1551 h	L.f.5 might have continued foraging for more than 15 trips but observations terminated before. She resumed next day. T: 29.4–31.8°, RH: 52–69%
9.vi.2013 1252–1606 h	1302 h 3 Lc, 4 Lf	L.f.5 second day	returned 1325 h	44	1604 h	L.f.5 might have continued foraging for more than 44 trips (59 in 2 days) but observations terminated before. T: 28.6–29.0°, RH: 61–74%
10.vi.2013 1311–1550 h	1312 h 3 Lc, 7 Lf	L.f.3 sev- enth day	returned 1421 h	13	1522 h	L.f.3 absence for ½ h indicates that she stopped foraging after 13 trips (65 in 4 days over 1 week, absent 7–9 June). T: 29.3–30.6°, RH: 62–72%
11.vi.2013 1307–1435 h	None arrived		-	-	-	Rainy morning, heavily overcast later, and low T probable reasons for lack of foraging. T: 23.3–23.9°, RH: 75–81%
12.vi.2013 1254–1600 h	1301 h 1 Lc, 4 Lf	L.f.6 first day	1346 h	29	1557 h	L.f.6 might have continued foraging for more than 29 trips but observations terminated before; trips resumed next day. T: 25.7–26.0°, RH: 76–89%
13.vi.2013 1308–1521 h	1310 h 4 Lc, 13 Lf	L.f.6 second day	returned 1335 h	32	1520 h	L.f.6 might have continued foraging (61 trips in 2 days) but observations terminated before. T: 27.1–27.5°, RH: 71–78%
14.vi.2013 1218–1718 h	1221 h 5 Lc, 8Lf	None marked	-	-	-	Bees still foraging when observations discontinued. T: 25.8–30.2°, RH: 57–74%
15.vi.2013 0857–1250 h	0903 h 3 Lc, 4 Lf	L.f.7	0944 h	26	1126 h	L.f.7 absent for 1½ h indicates she stopped foraging after 26 trips. T: 27.2–31.7°, RH: 48–79%
16.vi.2013 0852–1608 h	1014 h 3 Lc, 11 Lf	None marked	-	-	-	Bees still foraging when observations discontinued. T: 26.5–32.9°, RH: 43–74%
17.vi.2013 0938–1500 h	0942 h 3 Lc, 8 Lf	L.c.8	1009 h	13	1148 h	L.c.8 absent for 3 h indicates that she stopped foraging after 13 trips. T: 28.6–33.0°, RH: 49–66%

Table 3 (continued).

Date, time of study	First arrival, total number of bees	Specimen code	Time when marked ¹	Number of trips	Time of last trip	Remarks
18.vi.2013 0914–1145 h	0922 h 2 Lc, 3 Lf	None marked	-	-	-	Bees still foraging when observations discontinued. T: 27.4–28.1°, RH: 68–73%
19.vi.2013 1456–1710 h	1528 h 1 Lf	None marked	-	-	-	Only 1 <i>L. furva</i> foraged, 19 trips, then observations discontinued (although not marked, regular behavior excludes other bees). Late observations and dark clouds probable reason for few bees. T: 28.1–31.2°, RH: 63–71%
20.vi.2013 0945–1612 h	1128 h 2 Lc, 4 Lf	None marked	-	-	-	Bees still foraging when observations discontinued. Rain 1022–1100 h, wind, sun, dark clouds alternating, probable cause for few bees. T: 27.1–29.6°, HR: 63–99%



Figures 12–15. Foraging *Lisotrigona*. (12) Red marked L.f.29 (arrow) returned from 650 m in 67 min, after ‘drinking-while-riding’ on my eye. (13) L.f.29 returned from 205 m in 20 min, after ‘drinking-while-riding’ on my run in the opposite direction. (14) *L. cacciae* sucking blood from a scratch on the author’s arm. (15) *L. furva* imbibing nectar from a flower of a litchi tree; note proboscis and small pollen load on hind tibia (arrows). Bars = 4 mm.

ciliae but 1.0–6.2 min, average 3.1 min ($n = 74$) when sucking from the inner eye corner. In *L. furva* tear drinking lasted 0.4–1.7 min, average 0.9 min ($n = 35$) on the lower lid/ciliae, but 1.0–5.3, average 2.2 ($n = 35$) from the inner corner. An occasional very long settling period lasted 7–9 min, but the bee was possibly not imbibing constantly. The round trip time lasted 1.5–7.5 min, average 3.3 min ($n = 138$) in *L. cacciae*, and 2–8 min, average 3.8 min ($n = 70$) in *L. furva*. On average a single worker of *L. cacciae* collected tears over a period of 3 h 15 min ($n = 37$) per day (including round trip time), but the maximum was 10 h 27 min, after having collected already for 9 h the previous day (L.c.40). In *L. furva* the average was 2 h 14 min ($n = 15$) and the maximum 5 h 38 min.

Question (3): Tear collecting occurred during all months of the year (Tables 1–2) and from my 21 consecutive days’ exposure to the bees (Table 3), it can be extrapolated that, weather permitting, tear collecting occurs daily throughout the year.

Question (4): From the number of *Lisotrigona* congregating each month at my eyes (Tables 1–3) it is evident that most *L. cacciae* came during the hot-dry season (23–36°C, 25–60% RH), with 91 to about 300 specimens a day, followed by the rainy season (23–34°C, 60–99% RH) with 6 to about 190 specimens a day, and the cool season (11–29°C, 50–80% RH), with 3–55 specimens a day, except during cold periods when no bee arrived (cf. question [5]). For *L. furva* the values were about 220–320, 100–280, and 3–64, respectively. The exceptionally high numbers of *L. furva*, about 420 and 250 on 30.i.2014 and 20.ii.2014, were evidently freak events due to abnormally hot and dry weather for the cold season, hence not further considered.

Table 4. Duration of tear drinking, sucking position, and duration of round trips of marked *Lisotrigona cacciae* (L.c.) and *L. furva* (L.f.) at human eyes. Round trip time = time interval between flying off and back to the eye, including disgorging time in the nest. Position at eye: lc = on lower ciliae, ic = at inner corner of eye, x = average.

Specimen code	Site, date, time of study	Duration of sucking (min) at eye and respective position	Duration of round trips (min)
L.c.14	A, 23.ix.2013 1028–1825 h	lc: 0.5–2.0 ($x = 1.05, n = 20$) ic: 1.5–4.5 ($x = 3.06, n = 11$)	2.5–7.5 ($x = 4.46, n = 31$)
L.c.15	A, 10.x.2013 1007–1805 h	lc: 0.6–3.0 ($x = 1.61, n = 35$) ic: 5 ($n = 1$)	1.5–4.0 ($x = 2.64, n = 36$)
L.c.20	A, 28.i.2014 1020–1745 h	lc: 0.4–1.6 ($x = 0.84, n = 9$) ic: 1.0–5.5 ($x = 2.29, n = 37$)	2–6 ($x = 3.03, n = 46$)
L.c.30	A, 27.iii.2014 1007–1509 h	lc: none ic: 1.5–6.2 ($x = 4.36, n = 25$)	2–6.3 ($x = 3.13, n = 25$)
L.f.3	B, 5.vi.2013 1125–1640 h	lc: 0.5 ($x = 0.5, n = 3$) ic: 1.5–2.5 ($x = 1.8, n = 10$)	2.5–8 ($x = 4.58, n = 13$)
L.f.7	B, 15.vi.2013 0944–1126 h	lc: 0.4–1.5 ($x = 1.06, n = 16$) ic: 1.0–2.2 ($x = 1.7, n = 9$)	2.0–4.5 ($x = 2.71, n = 25$)
L.f.17	C, 4.xii.2013 1108–1705 h	lc: 0.6–1.7 ($x = 0.86, n = 16$) ic: 1.1–1.5 ($x = 1.3, n = 2$)	3.1–7.7 ($x = 4.73, n = 18$)
L.f.21	C, 30.i.2014 1150–1810 h	lc: none ic: 1.5–5.3 ($x = 2.9, n = 14$)	2.5–5 ($x = 3.64, n = 14$)

The earliest *L. cacciae* (L.c.40, Table 1) to arrive at the eye was at 0755 h (21.vi.2014, sunrise 0547 h), the latest to leave (L.c.42) at 1847 h (20.vi.2014, sunset 1903 h), the earliest *L. furva* (unmarked, Table 2) to arrive was at 0748 h (26.vi.2014, sunrise 0548 h), the latest to leave at 1824 h (L.f.1, Table 3) (31.v.2013, sunset 1856 h). However, most *Lisotrigona* congregated at 13–15 h (not mentioned in Tables). Half a dozen or more *Lisotrigona* at the same time at one eye was no rarity (Figs. 1–3, 7, 12), and the maximum was over 30.

Table 5. Lowest temperature and time when *Lisotrigona furva* started flying out of their nest during the cold season.

Date	Temperature, time when first bee flew out	Day's min/max temperature	Remarks on weather
03.xii.13	23.0°C, 1017 h	18.5°C/24.5°C	Sunny
09.xii.13	22.4°C, 1023 h	17.5°C/26.0°C	Sun and clouds alternating
11.xii.13	22.0°C, 0943 h	19.4°C/24.5°C	Sun and clouds alternating
12.xii.13	22.4°C, 0931 h	20.2°C/27.2°C	Sun and clouds alternating
14.xii.13	23.3°C, 1057 h	20.6°C/26.2°C	Cloudy, night rains
15.xii.13	23.3°C, 1047 h	20.6°C/24.0°C	Only one bee flew out, rain came 1115–1445 h, darkish afterwards
16.xii.13	22.4°C, 1231 h	16.3°C/22.7°C	Only one bee flew out, sunny morning, cloudy afternoon
17.xii.13	No bee flew out	15.1°C/20.8°C	Sunny but temperature below nest leaving threshold
18.xii.13	No bee flew out	11.6°C/21.0°C	Sunny but temperature below nest leaving threshold
19.xii.13	No bee flew out	11.9°C/20.7°C	Mostly cloudy, temperature below nest leaving threshold
20.xii.13	No bee flew out	12.6°C/21.6°C	Sunny but temperature below nest leaving threshold
21.xii.13	No bee flew out	11.2°C/21.8°C	Sunny but temperature below nest leaving threshold
23.xii.13	No bee flew out	12.1°C/21.8°C	Sunny but temperature below nest leaving threshold
24.xii.13	22.1°C, 1322 h	11.2°C/23.1°C	Sunny
25.xii.13	22.0°C, 1318 h	12.6°C/22.9°C	Only one bee flew out, only once. Sun and clouds alternating
28.xii.13	No bee flew out	13.3°C/22.3°C	Mostly sunny, but temperature below nest leaving threshold
31.xii.13	22.1°C, 1240 h	13.5°C/23.8°C	Sun and clouds alternating, slight breeze at times
01.i.14	22.3°C, 1204 h	13.6°C/24.1°C	Weather data not noted
20.i.14	22.9°C, 1350 h	11.7°C/23.8°C	Sun and clouds alternated
24.i.14	22.9°C, 1350 h	9.9°C/24.4°C	Weather data not noted

Table 6. Earliest time when the first *Lisotrigona furva* flew out of her nest during the warmest mornings, and time of first visitation of the spider lily (*Hymenocallis caribaea*) by meliponine *Tetragonula hirashimai*. Lily not always in flower.

Date of observation, time of sunrise	Time, temperature when first <i>L. furva</i> flew out	Remarks on weather; earliest time when <i>T. hirashimai</i> on spider lily
13.vii.2013; 0554 h	0702 h; 24.5°C	Partly sunny, then dark
14.vii.2013; 0555 h	0715 h; 24.7°C	Sunny
15.vi.2014; 0546 h	0806 h; 24.8°C	Cloudy
16.vi.2014; 0547 h	0726 h; 25.6°C	Sunny
18.vi.2014; 0547 h	0733 h; 24.9°C	Clouds and sun alternating
19.vi.2014; 0547 h	0805 h; 24.7°C	Briefly very slight rain, then cloudy
03.vii.2014; 0550 h	0810 h; 25.2°C	Clouds and sun alternating; 0610 h <i>T. hirashimai</i> on lily
04.vii.2014; 0551 h	0747 h; 25.0°C	Mostly sunny; 0610 h <i>T. hirashimai</i> on lily
06.vii.2014; 0551 h	0758 h; 25.6°C	Cloudy; 0606 h <i>T. hirashimai</i> on lily
10.vii.2014; 0553 h	0736 h; 24.5°C	Clouds and sun alternating; 0629 h <i>T. hirashimai</i> on lily
11.vii.2014; 0553 h	0755 h; 25.4°C	Cloudy
12.vii.2014; 0553 h	0819 h; 25.5°C	Slightly overcast; 0614 h <i>T. hirashimai</i> on lily
13.vii.2014; 0554 h	0802 h; 25.3°C	Heavily overcast
16.vii.2014; 0555 h	0840 h; 25.7°C	Sunny
25.vii.2014; 0559 h	0836 h; 25.7°C	Sunny

Question (5): The lowest temperature when *L. furva* foragers flew out of their nest (nest-leaving threshold) was 22.0–23.3°C (Table 5). During “winters” colder than normal, as was the second half of December 2013, no *L. furva* flew out of her nest for 7 days in a row when maximum temperatures were 20.7°C–22.3°C (no bee watching made on 22 December, but maximum temperature was below the threshold). On less cold “winter” days, workers still waited until late morning or afternoon at 1350 h, to leave the nest. On such days only one or a few workers foraged for a short period. When extrapolated for study sites A, B, C, 300–400 m higher up than site D, the bees presumably remained nest-confined for 16 consecutive days, since maximum temperatures presumably were below 22°C from 16 to 31 December (based on a temperature decrease of 2°C per 300 m). Other meliponine species had lower thresholds, viz. 19°C–20°C in the somewhat larger *T. laeviceps*, and 17°C–18°C in the much larger *Tetri. apicalis*. The earliest time when *L. furva* left her nest during the period with the warmest early mornings was 1–2¾ h after sunrise (Table 6), even in sunny weather and temperatures 1.2°C–2.5°C above the flying-out threshold. She flew 1–2 h later than *T. hirashimai* (Table 6).

Question (6): The host-pursuit range of *L. furva* was 425, 350, 250 and 200 m. While I walked slowly back, no bee arrived until I reached an area 20–30 m from the study site. Lack of bees in this distance suggests that the nest probably was only 20–50 m away from the study site. Hence the foraging range may have been some 400 m or more, but not less than 210 m. The riding-while-drinking range was 650 m (L.f.29), 520 m (L.f.21), 350 m (L.f.28), 325 m

(L.f.39), 275 m (L.f.22), all in the same direction, but 205 m (L.f.29) and 195 m (L.f.21) in the opposite direction. Five bees (71.4%), viz. those that rode 650 m, 520 m, 325 m, 205 m, 195 m, returned to my eyes at the study site after an absence of 67 min, 46 min, 57 min, 20 min and 15 min, respectively. Two bees did not return (from 350 m, 275 m). Importantly, two bees returned from both directions, viz. L.f.29 from 650 and 205 m (Figs. 12, 13), and L.f.21 from 520 and 195 m. Hence the homing range may have been 500–600 m or more, but at any rate could not have been less than 425 m.

Additional Observations

Behavior before earliest “nest leaving”

About one hour after sunrise, the head of a *L. furva* cautiously appeared well inside the entrance tubelet of the nest, but soon retracted out of sight; this was repeated several times. She would then remain deeper inside, not visible for many minutes. As this behavior was repeated many times, she then increasingly advanced nearer the rim, to finally lean out of it with the antennae extended forwards, presumably to probe the air temperature, only to retract inside again, often out of sight, for short to long intervals of up to 30 min, before finally flying out.

Puddling and water collecting

Lisotrigona were never found to imbibe water from pool sides or wet sand at streams near site B, nor at water basins exposed at sites C and D. Stingless bees *T. laeviceps* and *T. hirashimai* were present at basins of both sites, *T. fuscobalteata* only at the latter and *Apis florea* F. only at the former, together with various wasps. The richest water sucking community was at wet sand near site B during the dry and early rainy season, with many hymenopterans (*A. cerana* F., occasionally *A. dorsata* F., many Halictidae, wasps), and lepidopterans (Lycaenidae, Nymphalidae, Papilionidae, Pieridae, etc.).

Flower visiting

The only flowers observed to be visited by *L. cacciae* and *L. furva* were litchi (*Litchi chinensis* Sonn.) (Fig. 15), longan (*Dimocarpus longan* Lour.), both frequently, Jamaican cherry (*Muntingia calabura* L.) occasionally, and *Tetrastigma baenzigerii* C. L. Li and *T. hookeri* (Lawson) Planchon, once each by *L. furva* only. The first three are trees, the latter two large lianas. Analysis of corbicular pollen from workers entering the nest at site D confirmed pollen from the former two, and the trees *Leucaena leucocephala* Lam. de Wit and *Sennia siamea* (Lmk.) Irwin & Barn. Several pollen species remained unidentified. Besides pollen, *L. chinensis* and *D. longan* also offer nectar, whereas *Le. leucocephala* and *S. siamea* have extrafloral nectaries. I have seen these visited by *Tetri. apicalis*. From the literature, *L. furva* has been collected from *Buddleja asiatica* Lour. and *Callistemon* sp. (MICHENER & BOONGIRD, in ENGEL [2000]), both shrubs to small trees. Remarkably, despite frequent checks, so far I have never seen *Lisotrigona* on the ground flora, plenty of which were present at site C and D, some perennially in flower and visited by many small Halictidae and Apidae such as *Ceratina* spp. and *Braunsapis hewittii* (Cameron). Hence *Lisotrigona* may be mainly canopy-feeders when foraging for pollen and nectar, as well as for water since dew will have formed there during the night.

Collecting other resources

Sucking of sweat from my head, hand or arms was far less frequent than lachryphagy and tended to occur when many bees congregated. In a few cases blood oozing from a scratch

was sucked (Fig. 14). In other rare cases the skin was bitten briefly, although one *L. furva* persistently bit the skin for several minutes, causing a tiny subcutaneous haemorrhage. But the mouthparts were evidently too weak to break the skin so no blood flowed out. Occasionally *L. furva* licked (but did not chew) peeled overripe banana.

Possible communication and recruiting

Following the arrival of the first bee at my eye, which required one min to 3 h 24 min after I had been waiting at the research site, the increase in number of visitors often tended to be exponential. On other occasions it occurred that after a few sucking bouts by the first *Lisotrigona* at my eyes, two of them arrived in quick sequence, possibly scout and recruit. Often the feeding spot felt burning while the bee was sucking or shortly before leaving, the burning sensation continuing for a minute or so after she left. Further, once satiated she often did not readily fly off but remained a second or two while moving her antennae and forelegs, sometimes slightly turning her head to the right or the left, then on leaving she caused a characteristic sensation to my lid/ciliae as if forcefully grasping them for an instant on take-off. All these movements may be for possible scent marking. However, *Lisotrigona* was never seen laying a scent trail. She appears to respond to so-called local enhancement (orientation toward visual presence of a bee): in-flying bees tended to settle near, adjacent or on top of a feeding bee, even when much free space was available. At times a worker mistakenly settled on my temple where I have a dark mole the size of a *Lisotrigona*, often to be joined by further misguided foragers.

DISCUSSION

With up to 144 tear collecting trips in a day by a single worker (L.f.58), up to 10½ hours of daily tear foraging (L.c.40), for up to at least four days (L.f.3), there is little doubt that lachrymation is not for individual, but for nest requirements in *Lisotrigona*. The rare presence of minor amounts of pollen on tear drinkers indicates that in *Lisotrigona* there is division of labor where some workers fulfill a specialized function: tear collecting. Hitherto this task had not been fully appreciated although it is comparable to pollen, nectar or water collecting. Tear harvesting requires a high degree of adaptation for a bee. Namely, the ability to find a live vertebrate host, to approach rather than flee it, pursue it if it walks away, locate its eyes, gently land, furtively steal its tears for 0.5 to 6 minutes, persist when being jerked up and down by the host's eye blinking, hang on if it runs, and renew attacks if chased off. All of this could hardly be in more plain view of the victim and on its most sensitive organ. Also, *Lisotrigona* evidently recruit nest mates (see below) and probably scent-mark the feeding spot. Weather and climate permitting, tear harvesting is daily and year-round, even when permanent water is available, may continue during light rain drizzle and resume after an interruption due a downpour. More than 300 collectors may be involved in the course of a day, normally several at the same time and a maximum of over 30 at the same eye (all Figs.). What is so special in tears to have led to such a specialization? It is unlikely that salt is required in such amounts and it would be much easier to collect from human skin as sweat, as in fact many meliponines do including, in minor numbers, *Lisotrigona*. Water is used by *Apis* spp. for cooling their nest when outside temperatures are too high (e.g. LINDAUER, 1954) but nest cooling by water evaporation does not occur in meliponines (ROUBIK, 1989). Moreover, habitat temperature at study sites only oc-

asionally exceeded 33°C and reached a maximum of 35.7°C only once. This does not exceed the maximum brood chamber temperature which ranged 33.3°C–36.2°C in neotropical *Trigona spinipes* (F.) (ZUCCHI & SAKAGAMI, 1972), and is below 38.5°C and 40°C when 0% and 50% mortality, respectively, was registered in *Scaptotrigona postica* (Latreille) (MACIEIRA & PRONI, 2004). Finally, water is most important for diluting honey for larval feeding, but at the study sites water was always present and more easily accessible at places other than eyes, nevertheless sucked only by meliponines other than *Lisotrigona*. Tear drinking was resumed even after sustained rain had drenched the habitat, hence they were seeking something other than water. BÄNZIGER (1973) emphasized that lachrymation is special in having a high protein content. It is over two hundred times that present in sweat: 6.70 mg and 0.028 mg in 1 ml, respectively (RAUEN, 1964). This is generally overlooked, probably because both fluids contain salt, the assumed sole reason for imbibing them. The uptake of salts and other minerals from soil or skin by various bees is well known (e.g. SCHWARZ, 1948; BARROWS, 1974). But many bees also visit organic resources such as faeces, urine, cadavers, food left-overs, fluids from washings (ROUBIK, 1989 and references therein, and own observations). The most remarkable are three species of *Trigona*, *Tri. crassipes* (F.), *Tri. hypogea* Silvestri and *Tri. necrophaga* Camargo & Roubik, which have become obligatorily necrophagous (ROUBIK, 1982a; BAUMGARTNER & ROUBIK, 1989; CAMARGO & ROUBIK, 1991), and occasionally even predatory (MATEUS & NOLL, 2004). The intake by, and function in, stingless bees, moths and flies, males and/or females, of all these fluids has been reviewed and discussed in some detail (BÄNZIGER, 1973; BÄNZIGER *ET AL.*, 2009). Hence the observed preference for tears is not that surprising. In fact, lachrymation contains more proteins than the nectars richest in amino acids (the derivatives of proteins), viz. up to 3.9 mg/ml (0.39%) in nectar (BAKER & BAKER, 1975). Nevertheless, pollen is much richer in proteins and lipids, viz. 6–28% and 1–20% (WINSTON, 1987) versus 0.67%, and ‘very low’ in tears (RAUEN, 1964), respectively. However, tears are superior to pollen in four respects. First, digestion of pollen proteins is hampered because pollen grains are protected by hard and undigestible exine walls; digestion is via the germination pore or through ruptures in the walls caused by osmotic shock (WINSTON, 1987 and references therein). In tears the proteins are naturally dissolved and digestion can proceed promptly. Second, pollen harvesting is energetically more costly than tear collecting. For instance, when the meliponine *T. hirashimai* harvested pollen from spider lilies at site D, on average she had to be airborne for about 2/3 of the visiting time to transfer pollen from body and appendages to her corbiculae (BÄNZIGER, unpublished). *Lisotrigona* remain settled while drinking tears which they store in their crop in the very extensible metasoma, to twice its length and much enlarged in width compared to the empty crop (Figs. 10, 11). Moreover, transporting crop loads is energetically more economical than corbicular loads because fewer trips are required, at least in *Apis*, since a full crop load averages 50% of the body weight (maximum up to 90%), whereas corbicular loads average 10–36% (MICHENER, 1974; NICOLSON, 2009). Third, pollen in flowers is limited. When it becomes scarce, *T. hirashimai* may invest 15 to 45 min to gather the last grains (BÄNZIGER, unpublished). Tears are secreted continuously (30–120 µl/h [MILLODOT, 2009] under normal conditions but this can be increased many fold if irritated) to lubricate the eye surface, hence present in virtually unlimited amounts for tiny *Lisotrigona* which require only 0.5 to 6 min to acquire a full crop load. Fourth, besides the mentioned nutritional aspects, tears have also antiseptic properties. In human tears 21–25% of the total protein content is lysozyme, with minor amounts of beta-lysin, lactoferrin, gamma-globulin (FORRESTER *ET AL.*, 2008; MILLODOT, 2009), all with antibacterial activity. Although it seems unlikely that *Lisotrigona*’s principal

target is these bactericidal enzymes, their presence in tears in significant amounts is likely to provide an additional advantage (see below).

The fate of the tears once the collector delivered them to the nest has yet to be studied. Presumably tears are regurgitated to receiver bees so the collector can resume harvesting without delay—time between leaving and returning to eyes was 1.5–8 min only. Depending on the nest's requirements, tears may then be used directly for diluting honey to make a protein-enriched larval nutrient medium in the brood cells, it may be eaten by nurse bees for the production of glandular secretions to be mixed with pollen and honey as larval food, or it might be stored. Although plain water cannot be stored by *Apis* (MICHENER, 1974), there are reports that occasionally it is (NICOLSON, 2009). Thanks to the bactericidal enzymes they contain, tears may not need to be treated antibiotically to prevent spoilage as with pollen and nectar (GILLIAM *ET AL.*, 1985; GILLIAM *ET AL.*, 1990). Tears added to pollen and/or honey pots would only need to be concentrated by evaporation. Tears are of animal origin like the carrion derivatives exploited by the necrophagous *Tri. hypogea* group, but unlike aseptic tears, carrion is rich in microorganisms, is solid and has to be masticated and hydrolyzed by glandular secretions into slurries for transportation before mutualistic bacteria degrade it further. At the same time, competing spoilage microbes in storage pots and brood cells need to be controlled (ROUBIK, 1982a; GILLIAM *ET AL.*, 1985; GILLIAM *ET AL.*, 1990; CAMARGO & ROUBIK, 1991; SERRÃO *ET AL.*, 1997; NOLL *ET AL.*, 1997; MATEUS & NOLL, 2004). In this respect tears are also superior to cadavers.

The cases of the *Centris* bees visiting turtle and caiman eyes (DANGLES & CASAS, 2012; DE LA ROSA, 2014) are probably different from *Lisotrigona*. Anthophorini bees are not eusocial. Those *Centris* may have been males, the sex most frequently found exhibiting lachryphagy and the related puddling behavior among insects (e.g. ARMS *ET AL.*, 1974; ADLER & PEARSON, 1982; BECK *ET AL.*, 1999; MOLLEMAN *ET AL.*, 2005; BÄNZIGER *ET AL.*, 2009). They may have visited the reptiles for their own individual benefit. Possibly *Centris* primarily required salts since like other bees they need to replenish ions lost during excretion of surplus metabolic water (BERTSCH, 1984).

Lisotrigona's much shorter imbibing time when settled on the lower eye lid than at the inner corner of the eye—by a factor of more than two—seems to be due to the greater amount of tears assembling in the trench between eyeball and lid than at the higher-set eye corner where the tear-draining canaliculi are set. On the other hand, at the inner corner the foragers are more comfortably settled because they are not jerked every time the eye blinks. Also, less landing precision is required to reach the eye corner than the lid; when landed somewhat off the eye the bee can easily crawl the distance to the eye corner, whereas to crawl to the lid she has to push herself through or over the ciliae fringing the lid. Lack of competition in *Lisotrigona* at eyes (e.g. bees on top of other bees, Figs. 1, 7) is interesting, especially when compared to the sophisticated aggression strategies of the extirpating *Tri. spinipes* (Lepelletier) (NIEH *ET AL.*, 2005). The eye is a most unorthodox ecological niche where minuteness and gentleness is a precondition. Since in N. Thailand only two species would have to compete at a virtually inexhaustible source, tear sipping is likely to be peaceful.

Lisotrigona's nest-leaving threshold temperature of 22–23.3°C (Tab. 5) was clearly higher than in the somewhat larger *T. laeviceps* and the much larger *Tetri. apicalis* by some 2°C and 4°C, respectively. This is likely due to the fact that smaller species have a larger body surface relative to their body mass than larger species. Hence they are more exposed to chills and will leave the nest at a higher temperature to reduce the risk of undercooling. Interestingly, *L.*

cacciae L.c.19 and L.c.20 continued tear collecting four and two times after the temperature fell below the nest-leaving threshold in the evening of 7.xii.2013 and 28.i.2014, respectively. This suggests that they continued foraging because they had been “kept warm” (36°C) by the host’s eye and tear harvest in their crop.

On the other hand, there appears to be no obvious explanation for *L. furva*’s erratic earliest nest-leaving time in summer when the temperature was always above the fly-out threshold (Table 6). It was not correlated to bright or cloudy weather, nor to sunrise time. Additionally, there seems to be no reason why the bees’ earliest nest-leaving time was so late, 1–2 hours later than in *T. hirashimai* (Table 6). Two other features remain unresolved. First, some colonies seem to exhibit a much less pronounced lachryphagy, apparently unrelated to external factors, e.g., as found with the nest at site D. Second, as mentioned by BÄNZIGER & BÄNZIGER (2010), lachryphagy does not occur in the direct vicinity of the bees’ own nest (but can occur near the nest of another colony of the same species).

The length of time I had to wait until the first tear drinker arrived at my eye at site A was remarkably different in February to May from that of June to January, viz. 5 to 9 min versus 55 min to 3 h 24 min, respectively (Table 1). The most likely explanation is the prevailing seasonal wind direction – downwind from my study spot towards the nest (position unknown) during the dry-hot season but upwind during the other seasons. However, there were three exceptions during the rainy season. On 14.viii.2013 the time span was only 13 min – possibly the result of an irregularity in wind direction. But on 21.vi.2014 and 18.vii.2014, the brief time span of 9 min and 10 min probably was due to the memory of L.c.40 and L.c.45, respectively. On the preceding 20.vi. and 17.vii. the marked bees had sucked 67 and 64 times, respectively, so it is likely that they remembered the presence of the resource and returned to the site on the second day early, even in the absence of an odor plume. But the waiting time can be as short as 1 or 2 min (L.f.3 on 10.vi.2013, L.f.6 on 13.vi.2013), presumably for the same reason. Most probably, *Lisotrigona* bees locate hosts from long-distance (up to dozens of meters) by their body odors. When closer (a few meters or less), they are probably guided by sight combined with tear odors. The mentioned zig-zag flight (see Results) when near the eye indicates that the bee is following a scent plume. The gradual reduction of the zig-zag approach on subsequent visits indicates that they are increasingly guided by sight. BIESMEIJER *ET AL.* (2005) have shown experimentally that flower-visiting stingless bees (several Neotropical species of *Melipona* and other genera) have a spontaneous preference for dark centres, radiating stripes and peripheral dots as nectar guides. This is curiously similar to the eye of humans and many animals: the black pupil and often dark iris contrasting with the white sclera or pale pelage (many ungulates) or skin (tortoises), and the radially set ciliae (where present). This is likely to help in locating the eye. In fact, the spontaneous preference may even have been a preadaptation facilitating the evolution of lachryphagy in *Lisotrigona*.

That the largest congregations of tear collectors occurred during the hot-dry season is not surprising. Although this study argues that tears are harvested mainly for their proteins, tears contain much water so they concomitantly also replenish the dearth ensuing from higher water evaporation in the hot-dry season. During such periods lachryphagy may be more for water than proteins. Whether salt might additionally help retain water in the bees apparently has not been studied. Nevertheless, increased tear collecting not only can replenish water but also cover the required increase of protein needs caused by higher metabolic rates, including faster larval growth and adult activity, as a result of higher temperature.

The unexpected low turnout of *L. cacciae* at my eyes on 14.viii.2013, 18.vii.2014 and 13.viii.2014 could be due to inclement weather. On the other hand, the very few *L. cacciae* (9 on 23.ix.2013, 6 on 10.x.2013, and 5 on a recent check on 28.ix.2016), as well as a more or less gradual reduction in numbers (somewhat less evident in *L. furva*) as the rainy season progressed towards its peak (about mid-September to mid-October), appears not to be incidental. It can be ascribed to concomitant reduced flowering, causing colony reserves of honey and pollen to decline, at times to near nil, with decrease in foraging by *Melipona favosa* F. and *M. fulva* Lepeletier (ROUBIK, 1982b).

NIEH & ROUBIK (1995), NIEH (2004) and BIESMEIJER & SLAA (2004) reviewed the complex systems by which meliponines communicate food location. Behavioral elements suggesting communication among *Lisotrigona* have been mentioned under this heading in the results. There evidently must be some form of recruiting in *Lisotrigona* as indicated by the exponential increase in arrivals after the first *Lisotrigona* had come. Further, the feeling of a burning at the sucking site, often continuing after the bee had left, may indicate that a substance had been deposited, possibly a secretion by the mandibular glands to mark the site, e.g. when she turned her head sideways just before take-off. For instance, NIEH ET AL. (2003a) described *Tri. hyalinata* (Lepeletier) rubbing their mandibles against sugar feeders to odor-mark the site. In addition, a secretion of the tarsal glands might have been applied when before take-off *Lisotrigona* forcefully grasped my ciliae/lid, although she could have done this to better catapult herself into flight. An example of tarsal gland 'footprint' marking is *M. seminigra* Friese (HRNCIR ET AL., 2004). When two *Lisotrigona* arrived in rapid sequence it is also possible that an experienced forager piloted a recruit which followed her closely to my eye by sight, perhaps additionally guided by an aerial scent plume released by the forager in flight. Such a scenario has been suggested by LINDAUER & KERR (1958) for *M. quadrifasciata* (Lepeletier) and *M. scutellaris* Latreille, and by KERR (1969) for *Partamona cupira* (Smith). *Lisotrigona* squeezed between fingers occasionally release a very strong odor (BÄNZIGER, unpublished observation) which may serve this purpose. No *Lisotrigona* was seen laying scent trails as found in *Tri. ruficornis* Smith and *Scaptotrigona* sp. (LINDAUER & KERR, 1958), or *Scaptotrigona* sp. aff. *depilis* Moure (SCHMIDT ET AL., 2003). Nor was any evident wagging, spinning or extruding of anal droplets as described by NIEH ET AL. (2003b) for *M. mandacaia* Smith noticed. They show that by these acts this bee deposits odor cues, including a ventro-abdominal odor, and the spinning possibly helps it to learn local landmarks. Anal excretions as scent marks had also been studied by AGUILAR & SOMMEIJER (2001) in *M. favosa*. Interestingly, expelling anal droplets has been described also for some tear drinking moths (REID, 1954). Eulachryphagous nolid moth *Lobocraspis griseifusa* Hampson exudes a droplet of 1.5 mm diameter every 6–7 sec for up to 2 h, a total of nearly 2 cc when sucking at eyes of unguulates (BÄNZIGER, 1973). But the function is different, viz. a filtering process for concentrating tear proteins and expelling water and salts.

The present maximum foraging range of *L. furva*, possibly some 400 m or more but not less than 210 m, and her homing range, possibly some 600 m or more but not less than 425 m, are two to three times previous estimates (BÄNZIGER ET AL., 2009). In fact, there are strong indications that *L. furva* must have foraging and homing capabilities greater than these and well above size-comparable pollen and nectar foragers, a possible result of adaptation to ephemeral and mobile sources. First, the maximum foraging range of *T. iridipennis* (Smith) was only 120 m (LINDAUER, 1956) although this species is larger. Flight distance has been shown to be

positively correlated to body and wing size in stingless bees (ARAÚJO *ET AL.*, 2004). Second, the success rates of returning to the nest from maximum distance in *M. fasciata* Latreille and *Tri. capitata* Smith, and in the bumblebee *Bombus terrestris* (L.), all much larger than *Lisotrigona*, were only 19.7%, 9.6%, and 25.5%, respectively (ROUBIK & ALUJA, 1983; GOULSON & STOUT, 2001). In *L. furva* it was 71.4%. Third, return time to the nest in bumblebees was 6 hours to 9 days (no return time measured in the study of ROUBIK & ALUJA, 1983). Return time to my eyes in *L. furva* was no more than 67 min, including time for traveling to the nest and regurgitating my tears.

The presence of a host within *Lisotrigona*'s range needs not be ephemeral but can last as long as the flowering of a tree. Some mammals and birds can be nest-bound for weeks when rearing their young. They may regularly visit, often in flocks, salt licks, water holes, and trees in fruit. Ruminating ungulates may lie down for hours. Human hunter-gatherers stay at improvised shelters for weeks. Some early humans frequented or lived in limestone caves for generations. Interestingly, many meliponines have a predilection for nesting in cavities accessed through small fissures in limestone rock faces (BÄNZIGER *ET AL.*, 2011). In fact, lachryphagy in meliponines may have originated in association with humans (first appeared 10⁵–10⁶ years ago), perhaps as a specialization derived from sweat sucking—humans are the only mammals secreting sweat in large amounts (with partial exceptions such as hippopotamuses and, in very small amounts, tree shrews and some primates [BURNS *ET AL.*, 2010]). Nowadays *Lisotrigona* may have few chances to repeatedly snatch tears from sensitive “civilized” humans (some masochistic scientist excepted), but tropical forest natives are so hardened to mosquitoes and other scourges that they will tolerate tear sipping bees as a rather minor nuisance. In an older evolutionary alternative, lachryphagy might have developed in association with large mammals and birds some 30–70 mya. Since these virtually do not secrete sweat, meliponines might initially have been attracted to eyes as a source of water in dry regions or seasons. In this scenario tear sucking may have derived primarily from the bees' water collecting.

ACKNOWLEDGMENTS

I am very grateful to the late C. D. Michener for his constant encouragement, as well as for making me aware of his article of 2010 (with Rasmussen). R. Beaver improved the English. For finding and sending crucial references I am indebted to M. Burgett, with whom I had many fruitful discussions on bees. He, R. Solis, W. Brockelman and C. Praz helped with the manuscript. My wife Saengdao helped me with complex computer matters. A. Kocyan, D. W. Roubik, M. J. Toda, Ms. M. Kankonsue, and Ms. E. Frey also found important references.

REFERENCES

- ADLER, P. H., AND D. L. PEARSON. 1982. Why do male butterflies visit mud puddles? *Can. J. Zool.* 60: 322–325.
- AGUILAR, I., AND M. SOMMEIJER. 2001. The deposition of anal excretions by *Melipona favosa* foragers (Apidae: Meliponinae): behavioural observations concerning the location of food sources. *Apidologie* 32: 37–48.
- ARAÚJO, E. D., M. COSTA, J. CHAUD-NETTO, AND H. G. FOWLER. 2004. Body size and flight distance in stingless bees (Hymenoptera: Meliponini): Inference of flight range and possible ecological implications. *Braz. J. Biol.* 64(3B): 563–568.
- ARMS, K., P. FEENY, AND R. C. LEDERHOUSE. 1974. Sodium: stimulus for puddling behavior by Tiger Swallow butterflies, *Papilio glaucus*. *Science* 185: 372–374.

- BAKER, H. G., AND I. BAKER. 1975. Studies of nectar-constitution and pollinator-plant coevolution. Pages 100–140 in L. E. Gilbert and P. H. Raven (eds.), *Coevolution of animals and plants*. University of Texas Press, Austin.
- BÄNZIGER, H. 1973 [1972]. Biologie der lacriphagen Lepidopteren in Thailand und Malaya. *Rev. suisse Zool.* 79: 1381–1469.
- BÄNZIGER, H. 1988. The heaviest tear drinkers: Ecology and systematics of new and unusual notodontid moths. *Nat. Hist. Bull. Siam Soc.* 36: 17–53.
- BÄNZIGER, H. 1995. *Microstega homocolorum* sp. n. – the most frequently observed lachryphagous moth of man (Lepidoptera, Pyralidae: Pyraustinae). *Rev. Suisse Zool.* 102: 265–276.
- BÄNZIGER, H., S. BOONGIRD, P. SUKUMALANAND, AND S. BÄNZIGER. 2009. Bees (Hymenoptera: Apidae) that drink human tears. *J. Kansas Entomol. Soc.* 82: 135–150.
- BÄNZIGER, H., AND S. BÄNZIGER. 2010. Mammals, birds and reptiles as hosts of *Lisotrigona* bees, the tear drinkers with the broadest host range (Hymenoptera, Apidae). *Mitt. schweiz. entomol. Ges.* 83: 271–282.
- BÄNZIGER, H., S. PUMIKONG, AND K. SRIMUANG. 2011. The remarkable nest entrance of tear drinking *Pariotrigona klossi* and other stingless bees nesting in limestone cavities (Hymenoptera: Apidae). *J. Kansas Entomol. Soc.* 84: 22–35.
- BARROWS, E. M. 1974. Aggregation behavior and response to sodium chloride in females of a solitary bee, *Augochlora pura* (Hymenoptera: Halictidae). *Florida Entomol.* 57: 189–193.
- BAUMGARTNER, D. L., AND D. W. ROUBIK. 1989. Ecology of necrophilous and filth-gathering stingless bees (Apidae: Meliponinae) of Peru. *J. Kansas Entomol. Soc.* 62: 11–22.
- BECK, J., E. MÜHLENBERG, AND K. FIEDLER. 1999. Mud-puddling behavior in tropical butterflies: in search of proteins or minerals. *Oecologia* 119: 140–148.
- BERTSCH, A. 1984. Foraging in male bumblebees (*Bombus lucorum* L.): maximizing energy or minimizing water load. *Oecologia* 62: 325–336.
- BIESMEIJER, J. C., M. G. L. VAN NIEUWSTADT, S. LUKÁCS, AND M. L. SOMMEIJER. 1998. The role of internal and external information in foraging decisions of *Melipona* workers (Hymenoptera: Meliponinae). *Behav. Ecol. Sociobiol.* 42: 107–116.
- BIESMEIJER, J. C., AND E. TÓTH. 1998. Individual foraging, activity level and longevity in the stingless bee *Melipona beecheii* in Costa Rica (Hymenoptera, Apidae, Meliponinae). *Insectes soc.* 45: 427–443.
- BIESMEIJER, J. C., AND H. DE VRIES. 2001. Exploration and exploitation of food sources by social insect colonies: a revision of the scout-recruit concept. *Behav. Ecol. Sociobiol.* 49: 89–99.
- BIESMEIJER, J. C., AND E. J. SLAA. 2004. Information flow and organization of stingless bee foraging. *Apidologie* 35: 143–157.
- BIESMEIJER, J. C., M. GIURFA, D. KOEDAM, S. G. POTTS, D. M. JOEL, AND A. DAFNI. 2005. Convergent evolution: floral guides, stingless bee nest entrances, and insectivorous pitchers. *Naturwissenschaften* 92: 444–450.
- BOONGIRD, S. 2010. *Beekeeping with European honey bee and small stingless bees*. Ramkhamhaeng Univ. Press, Bangkok. 133 pp. (in Thai)
- BOONTOP, Y., S. MALAIKAN, K. CHAREANSOM, AND D. WIWATWITAYA. Diversity of stingless bees (Apidae: Meliponini) in Thong Pha Phum District, Kanchanaburi Province, Thailand. *Kasetsart J. (Nat. Hist.)* 42: 444–456.
- BURNS, T., S. BREATHNACH, N. COX, AND C. GRIFFITHS. 2010. *Rook's Textbook of Dermatology*. 8th edition. Wiley-Blackwell, Oxford. 4432 pp.
- BÜTTIKER, W. 1973. Further records of eye-frequenting Noctuidae (Lepidoptera) from South Africa. *S. African J. Sci.* 69: 337–341.
- BÜTTIKER, W., AND J. A. WHELLAN. 1966. Records of eye-frequenting moths from Rhodesia. *Rhodesia Agric. J.* 63: 24–27.
- CAMARGO, J. M. F., AND S. R. M. PEDRO. 2003. Meliponini neotropicais: o gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae) – bionomia e biogeografia. *Rev. Bras. Entomol.* 47: 311–372.
- CAMARGO, J. M. F., AND S. R. M. PEDRO. 2004. Meliponini neotropicais: o gênero *Ptilotrigona* Moure (Hymenoptera, Apidae, Apinae). *Rev. Bras. entomol.* 48: 353–377.
- CAMARGO, J. M. F., AND D. W. ROUBIK. 1991. Systematics and bionomics of the apoid obligate necrophages: the *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biol. J. Linn. Soc.* 44:13–39.
- CHUTTONG, B., Y. CHANBANG, K. SRINGARM, AND M. BURGERTT. (2015). Physicochemical profiles of stingless bee (Apidae: Meliponini) honey from South East Asia (Thailand). *Food Chem.* 192: 149–155.
- CONTRERA, F.A. L., AND J. C. NIEH. 2007. Effect of forager-deposited odors on the intra-patch accuracy of recruitment of the stingless bees *Melipona panamica* and *Partamona peckolti* (Apidae, Meliponini). *Apidologie* 38: 584–594.

- DANGLES, O., AND J. CASAS. 2012. The bee and the turtle: a fable from Yasuni National Park. *Front. Ecol. Environ.* 10: 446–447.
- ENGEL, M. S. 2000. A review of the Indo-malayan meliponine genus *Lisotrigona*, with two new species (Hymenoptera: Apidae). *Orient. Insects* 34: 229–237.
- FORRESTER, J. V., A. D. DICK, P. G. McMENAMIN, AND F. ROBERTS. 2008. *The eye. Basic sciences in practice*. 3rd ed. Saunders, Edinburgh. 540 pp.
- GILLIAM, M., S. L. BUCHMANN, B. J. LORENZ, AND D. W. ROUBIK. 1985. Microbiology of the larval provisions of the stingless bee, *Trigona hypogea*, an obligate necrophage. *Biotropica* 17: 28–31.
- GILLIAM, M., D. W. ROUBIK, AND B. J. LORENZ. 1990. Microorganisms associated with pollen, honey, and brood provisions in the nest of a stingless bee, *Melipona fasciata*. *Apidologie* 21: 89–97.
- GOULSON, D., AND J. C. STOUT. 2001. Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera: Apidae). *Apidologie* 32: 105–111.
- HALL, R. D., AND R. R. GERHARDT. 2002. Flies (Diptera). Pages 127–145 in G. Mullen and L. Durden (eds.), *Medical and Veterinary Entomology*. Academic Press, California.
- HRNCIR, M., S. JARAU, R. ZUCCHI, AND F. G. BARTH. 2004. On the origin and properties of scent marks deposited at the food source by a stingless bee, *Melipona seminigra*. *Apidologie* 35: 3–13.
- INSON, C., AND S. MALAIPAN. 2006. Diversity of stingless bees (Apidae: *Trigona* spp. and *Hypotrigona* spp.) and their resin and gum collecting behavior from nature in Golden Jubilee Thong Pha Phum Project, Thong Pha Phum District, Kanchanaburi Province. *BRT Res. Rep.* 2006: 20–31. (in Thai)
- KERR, W. E. 1969. Some aspects of the evolution of social bees (Apidae). Pages 119–175 in T. Dobzhansky, M. K. Hecht, and W. C. Steere (eds.), *Evolutionary Biology*, Vol. 3, Appleton-Century-Crofts, New York.
- KHAMYOTCHAI, K., H. BÄNZIGER, AND J. KULSARIN. 2015. Nest entrance architectural types of *Tetragonula laeviceps* (Smith), a stingless bee species complex (Hymenoptera: Apidae: Meliponini) in Thailand and Peninsular Malaysia. *J. Agric.* 31: 1–9. (in Thai)
- KLAKASIKORN, A., S. WONGSIRI, S. DEWANISH, AND O. DUANGPHAKDEE. 2005. New record of stingless bees (Meliponini: *Trigona*) in Thailand. *Nat. Hist. J. Chulalongkorn Univ.* 5: 1–7.
- LINDAUER, M. 1954. Temperaturregulierung und Wasserhaushalt im Bienenstaat. *Zeitschr. f. vergl. Physiol.* 36: 391–432.
- LINDAUER, M. 1956. Über die Verständigung bei indischen Bienen. *Zeitschr. f. vergl. Physiol.* 38: 521–557.
- LINDAUER, M., AND W. E. KERR. 1958. Die gegenseitige Verständigung bei den stachellosen Bienen. *Zeitschr. f. vergl. Physiol.* 41: 405–434.
- MÁCA, J., AND D. OTRANTO. 2014. Drosophilidae feeding on animals and the inherent mystery of their parasitism. *Parasites & Vectors*, doi:10.1186/s1307101405164
- MACIEIRA, O. J. D., AND E. A. PRONI. 2004. Capacidade de resistência a altas e baixas temperaturas em operárias de *Scaptotrigona postica* (Latreille) (Hymenoptera, Apidae) durante os períodos de verão e inverno. *Rev. Bras. Zool.* 21: 893–896.
- MATEUS, S., AND F. B. NOLL. 2004. Predatory behavior in a necrophagous bee *Trigona hypogea* (Hymenoptera: Apidae, Meliponini). *Naturwissenschaften* 91: 94–96.
- MICHENER, C. D. 1974. *The social behavior of the bees. A comparative study*. Belknap Press of Harvard Univ. Press, Cambridge. 394 pp.
- MICHENER, C. D. 2000. *The bees of the world*. John Hopkins Univ. Press, Baltimore. 913 pp.
- MICHENER, C. D. 2007. *Lisotrigona* in Thailand, and the male of the genus (Hymenoptera: Apidae: Meliponini). *J. Kansas Entomol. Soc.* 80: 130–135.
- MICHENER, C. D., AND S. BOONGIRD. 2004. A new species of *Trigona* from peninsular Thailand (Hymenoptera: Apidae: Meliponini). *J. Kansas Entomol. Soc.* 77: 143–146.
- MILLODOT, M. 2009. *Dictionary of optometry and visual science*. 7th edition. Butterworth-Heinemann, Edinburgh. 465 pp.
- MINER, J. J., A. SENE, J. M. RICHNER, A. M. SMITH, A. SANTEFORD, N. BAN, J. WEGER-LUCARELLI, F. MANZELLA, C. RÜCKERT, J. GOVERO, K. K. NOGUCHI, G. D. EBEL, M. S. DIAMOND, AND R. S. APTE. 2016. Zika virus infection in mice causes panuveitis with shedding of virus in tears. *Cell Reports* 16: 3208–3218.
- MOLLEMAN, F., R. H. A. GRUNSVEN, M. LIEFTING, B. G. ZWAAN, AND P. M. BRAKEFIELD. 2005. Is male puddling behaviour of tropical butterflies targeted at sodium for nuptial gifts or activity? *Biol. J. Linn. Soc.* 86: 345–361.
- MOON, R. D. 2002. Muscid flies (Muscidae). Pages 279–301 in G. Mullen and L. Durden (eds.), *Medical and Veterinary Entomology*. Academic Press, California.
- NICOLSON, S. W. 2009. Water homeostasis in bees, with emphasis on sociality. *J. Experim. Biol.* 212: 429–434.
- NIEH, J. C. 2004. Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie* 35: 159–182.

- NIEH, J. C., AND D. W. ROUBIK. 1995. A stingless bee (*Melipona panamica*) indicates food location without using a scent trail. *Behav. Ecol. Sociobiol.* 37: 63–70.
- NIEH, J. C., F. A. L. CONTRERA, AND P. NOGUEIRA-NETO. 2003a. Pulsed mass recruitment by a stingless bee, *Trigona hyalinata*. *Proc. R. Soc. Lond. B* 270: 2191–2196.
- NIEH, J. C., S. RAMÍREZ, AND P. NOGUEIRA-NETO. 2003b. Multi-source odor-marking of food by a stingless bee, *Melipona mandacaia*. *Behav. Ecol. Sociobiol.* 54: 578–587.
- NIEH, J. C., K. KRUIZINGA, L. S. BARRETO, F. A. L. CONTRERA, AND V. L. IMPERATRIZ-FONSECA. 2005. Effect of group size on the aggression strategy of an extirpating stingless bee, *Trigona spinipes*. *Insectes Soc.* 52: 1–8.
- NOLL, F. B., R. ZUCCHI, J. A. JORGE, AND S. MATEUS. 1997 [1996]. Food collection and maturation in the necrophagous stingless bee, *Trigona hypogea* (Hymenoptera: Meliponinae). *J. Kansas Entomol. Soc.* 69: 287–293.
- OTRANTO, D., R. P. LIA, C. CANTACESSI, C. TESTINI, A. TROCCELLI, J. L. SHEN, AND Z. X. WANG. 2005. Nematode biology and larval development of *Thelazia callipaeda* (Spirurida, Thelaziidae) in the drosophilid intermediate host in Europe and China. *Parasitol.* 131: 847–855.
- RAJITPARINYA, T., M. TITAYAVAN, AND M. BURGETT. 2001. The ecology and diversity of stingless bees (Hymenoptera: Apidae) in Northern Thailand. Pages 91–95 in (no eds. mentioned), *Proc. Seventh Inter. Conf. Trop. Bees: Management and Diversity, and Fifth Asian Apic. Assoc. Conf.* The National Sci. Technol. Dev. Agency, Bangkok.
- RASMUSSEN, C., AND S. A. CAMERON. 2007. A molecular phylogeny of the Old World stingless bees (Hymenoptera: Apidae: Meliponini) and the non-monophyly of the large genus *Trigona*. *Syst. Entomol.* 32: 26–39.
- RASMUSSEN, C., AND J. M. F. CAMARGO. 2008. A molecular phylogeny and the evolution of nest architecture and behavior in *Trigona s.s.* (Hymenoptera: Apidae: Meliponini). *Apidologie* 39: 102–118.
- RASMUSSEN, C., AND S. A. CAMERON. 2010. Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal. *Biol. J. Linn. Soc.* 99: 206–232.
- RASMUSSEN, C., AND C. D. MICHENER. 2010. The identity and neotype of *Trigona laeviceps* Smith (Hymenoptera: Apidae). *J. Kansas Entomol. Soc.* 83: 129–133.
- REID, E. T. M. 1954. Observations on feeding habits of adult *Arcyophora*. *Proc. R. Entomol. Soc. Lond. B.* 23: 29–33.
- RAUEN, H. M. 1964. *Biochemisches Taschenbuch*. 2. Teil. Springer, Berlin. 1084 pp.
- ROSA, C. L. DE LA. 2014. Additional observations of lachryphagous butterflies and bees. *Front. Ecol. Environ.* 12: 210.
- ROUBIK, D. W. 1982a. Obligate necrophagy in a social bee. *Science* 217: 1059–1060.
- ROUBIK, D. W. 1982b. Seasonality in colony food storage, brood production and adult survivorship: studies of *Melipona* in tropical forest (Hymenoptera: Apidae). *J. Kansas Entomol. Soc.* 55: 789–800.
- ROUBIK, D. W., AND M. ALUIJA. 1983. Flight ranges of *Melipona* and *Trigona* in tropical forest. *J. Kansas Entomol. Soc.* 56: 217–222.
- ROUBIK, D. W. 1989. *Ecology and natural history of tropical bees*. Cambridge University Press, Cambridge. 514 pp.
- ROUBIK, D. W. 2006. Stingless bee nesting biology. *Apidologie* 37: 124–143.
- SAKAGAMI, S. F. 1978. *Tetragonula* stingless bees of the Continental Asia and Sri Lanka (Hymenoptera, Apidae) (*sic*). *J. Fac. Sci., Hokkaido Univ. Zool.* 21: 165–247.
- SÁNCHEZ, D., J. C. NIEH, AND R. VANDAME. 2008. Experience-based interpretation of visual and chemical information at food sources in the stingless bee *Scaptotrigona mexicana*. *Anim. Behav.* 76: 407–414.
- SCHMIDT, V. M., R. ZUCCHI, AND F. G. BARTH. 2003. A stingless bee marks the feeding site in addition to the scent path (*Scaptotrigona aff. depilis*). *Apidologie* 34: 237–248.
- SCHWARZ, H. F. 1939. The Indo-malayan species of *Trigona*. *Bull. Amer. Mus. Nat. Hist.* 76: 83–141.
- SCHWARZ, H. F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. *Bull. Amer. Mus. Nat. Hist.* 85: 1–546. (cited from ROUBIK, D. W. 1989)
- SERRÃO, J. E., C. DA CRUZ-LANDIM, AND R. L. M. SILVA-DE-MORAES. 1997. Morphological and biochemical analysis of the stored and larval food of an obligate necrophagous bee, *Trigona hypogea*. *Insectes soc.* 44: 337–344.
- SLAA, E. J., J. WASSENBERG, AND J. C. BIESMEIJER. 2003. The use of field-based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. *Ecol. Entomol.* 28: 369–379.
- THUMMAJITSAKUL, S., S. KLINBUNGA, D. SMITH, AND S. SITTIPRANEED. 2008. Genetic diversity and population structure of *Trigona pagdeni* Schwarz in Thailand. *Apidologie* 39: 446–455.
- VIT, P., S. R. M. PEDRO, AND D. W. ROUBIK (eds.). 2013. *Pot honey. A legacy of stingless bees*. Springer, New York. 655 pp.
- WINSTON, M. L. 1987. *The biology of the honey bee*. Harvard Univ. Press, Cambridge. 281 pp.
- ZUCCHI, R., AND S. F. SAKAGAMI. 1972. Capacidade termo-reguladora em *Trigona spinipes* e em algumas outras espécies de abelhas sem ferrão. Pages 301–309 in *Homenagem à Warwick E. Kerr*. Rio Claro, Brazil. (cited from MICHENER C. D. 1974)