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BRIEF COMMUNICATION

An unusually large and persistent male swarm of the stingless bee *Tetragonula laeviceps* in Thailand (Hymenoptera: Apidae: Meliponini)

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Abstract. At an entrance of a nest of *Tetragonula laeviceps* (Smith) located in Chiang Mai University campus we observed a male swarm that lasted for at least 40 consecutive days and contained more than 7000 males each time on several days. Surprisingly, harvesting the day's totality of males did not reduce the swarm size on the following day, thus indicating that most males swarmed only one day, at the end of which they presumably perished from exhaustion away from the nest. Males of other species were also found in the swarm, a behavior corroborated by previous observations with other species elsewhere in Thailand.

INTRODUCTION

A huge swarm of *Tetragonula laeviceps* (Smith) was first noted on 29 April 2013 in front of the nest entrance, when it was already in full swing, perhaps for several days. It was then checked virtually every day until the last day, 7 June 2013. The nest entrance was 2 m above ground, near the top of a hollow iron pillar of 18 cm in diameter connected to two hollow iron beams sustaining a roof, on the Chiang Mai University campus. At times several hundred males rested on the iron pillar in a dense cluster, but most were swarming. Sudden gusts of wind shifted and somewhat dispersed the swarm, but it soon reconvened. Rain disrupted the swarming. In 2013, rain came late during the typical rainy season, was uncommon, and mostly during early to midafternoon during the day. If rain lasted until around 16:00 h, generally no swarm reconvened that day. No audible wingbeat noise was perceived, even when standing in the middle of the swarm with thousands of males flying by our ears, nearly touching our heads. The silence was strangely odd – a swarm of some 100 males of *Tetragonilla collina* (Smith) observed elsewhere, produced a very weak, low-pitch sound, very un-

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like the buzzing one can hear at the nest entrance of other meliponines (Bänziger & Khamyotchai, pers. obs.).

On our first day of observations, about 750 males were collected around noon with a net (for exact identification and counting all collections had to be euthanized), but about two to three times more males were still flying. On 5 May observations were throughout the day. At 06:15 h (sunrise was at 05:54 h) no swarm was yet evident. A net was fixed over the nest entrance for trapping all bees leaving the nest and preventing any outsiders from entering. By 06:50 h some 50 workers were crawling inside the net and a few flying outside it (probably the few returnees which left the nest before the net was fixed). By 08:00 h there were well over 100 workers inside the net but no swarm yet outside the net. At 09:25 h a broad swarm of 20–40 males were flying around the iron pillar. At 09:30 h, in a trial sweep, 32 males and five workers of *T. laeviceps*, and one male of *Lepidotrigona terminata* (Smith) were collected. At 09:45 h only six bees had settled outside the net, all workers of *T. laeviceps*. By 11:00 h the swarm was already considerably large and a sweep trial yielded 568 males and six workers of *T. laeviceps*, and four males of *L. terminata*. The swarm continued to increase until well past 13:00 h. In order to assess the peak number, all bees were collected from 13:35 to 14:43 h. The result was 6212 males and 80 workers of *T. laeviceps*, 32 males of *L. terminata*, and two males of *Lisotrigona furva* Engel. Despite our efforts, some bees evaded and others joined in until 16:20 h when the swarm steadily diminished from 128 to 9 males at 17:10 h (sunset was at 18:47 h). The day's total amounted to 7248 males of *T. laeviceps*, 101 males of *L. terminata*, and two males of *Li. furva*. Virtually all males of *T. laeviceps* carried small amounts of sticky material on their metatibiae, probably propolis, as previously recorded by Boongird & Michener (2010). At 16:30 h the net covering the nest entrance was removed and all bees trapped inside collected for counting: there were 986 workers and two males of *T. laeviceps*.

Much to our surprise, the following day we found a new, similar-sized swarm. No collecting was done between 6 and 16 May. On 17 May, between 14:05 and 16:20 h, we collected again all bees flying in front of the nest entrance and counted a total of 1081 males of *T. laeviceps* but no other species. This time no net was fixed over the entrance; workers captured in the swarm were not counted. On the following day the swarm was about the same size as the previous day, as in the case of 5–6 May. On the following days, the swarm increased in size, being largest on 23 May (3–5 m in diameter). From 25 May onwards the swarm steadily decreased in diameter and number of individuals until 8 June, when no bees were seen flying. No male was ever seen entering the nest throughout the study period, though some rested about 20 cm or more from the nest entrance.

Four important findings are worth discussing. First, and perhaps the most surprising of all, is that on 6 and 18 May, the days following the capture of all males, viz 7248 and 1081 individuals respectively, a new and similar-sized swarm had reconvened. This suggests that most males appeared to swarm only one day at the nest, presumably subsequently perishing from exhaustion. However, we only found a tiny fraction of dead males on the ground around the nest entrance. None were found on the ground around the nearby trees. We also did not observe males roosting on branches and leaves of trees during the evening, as well as on the roof construct. During some evenings, only a very few males remained on the pillar. Thus, presumably the vast majority of males flew off and dispersed some distance from the nest. Our observations seem to be in contradiction with the findings of Galindo López & Kraus (2009). Those authors found that 90% of marked males of *Scaptotrigona mexicana*

(Guérin-Méneville) returned to congregate daily at the same colony for 15 days in Mexico. However, congregating *S. mexicana* are permanently settled at attractive colonies. They only fly off when disturbed and settle back in 5 to 10 minutes. Males of *T. laeviceps*, on the other hand, formed permanent swarms from morning until evening, every day, only part of the airborne males occasionally settling for a rest on the iron pillar. Their energy consumption must be conspicuous, rather higher than that of foragers but, unlike these, males cannot refuel at nests, and reports of males collected from flowers are so meager that it seems unlikely that much nectar sucking occurs. Moreover, flying time has more influence on the bees' lifespan than chronological age (Winston, 1987). Older bees are unable to synthesize glycogen for energy and when this is exhausted they perish. Having been airborne for much of a day, probably after flying a substantial distance before reaching a virgin queen nest, many males may simply not survive to congregate for a second day.

Second, only two males (0.03% of the day's total) were trapped inside the net fixed over the nest on 5 May, hence the vast majority of males must have come from other nests. This observation agrees with the finding of Cameron *et al*. (2004). Based on genetic analysis these authors found that males swarming at a nest of *T. collina* originated from 132 different colonies and none from the nest they were swarming at [but refer to the study on *T. fuscobalteata* (Cameron) by Boongird (2011)].

Third, the size and duration of the swarming is unheard of. It is commonly reported (*e.g*., Michener, 1974; Cortopassi-Laurino, 2007; Boongird & Michener, 2010; Bänziger & Khamyotchai, pers. obs.) that male swarms consist of a few dozen to several hundred males, generally lasting for a few days to a week or so. We found a few dozen to up to more than 7000 males swarming every day for 40 days. Since most males appeared to swarm only one day, the total number of males might be as much as 100,000. Whereas the two counts from 5 and 17 May were exact, the others were rough estimates but even 50,000 males is nearly beyond belief. A survey of the study area (300x650 m) revealed 23 nests of *T. laeviceps*, in addition to 18 of *L. terminata*, ten of *T. collina*, four of *Li. furva*, three of *Heterotrigona apicalis* (Smith), and one of *H. melanoleuca* (Cockerell). All these nests were found in 1075 trees with at least 15 cm in diameter. Sakagami *et al*. (1983) found 135 males and 1149 workers in a nest of Sumatran *T. laeviceps*, but large colonies containing several thousand workers have also been observed (Kasetsuntorn, pers. comm.; Khamyotchai, unpubl. data). Our nest may have had close to 10,000 workers, based on the assumption that the 986 foragers caught in the net over the nest entrance on 5 May represented 10% of the nest's workers (a frequently-used rough ratio foragers:workers). During the swarming season, large nests of *T. laeviceps* may thus contain between 500 and 1000 males. Further, according to a review on male meliponines (Velthuis *et al*., 2005), colonies undergo male-producing periods of short duration during which the percentage of males can be as high as 74% in a given comb in some species of *Melipona* Illiger, though more commonly 20–30%. These periods are not synchronized at the population level, so that peaks with high male numbers can occur over longer periods during the swarming season of a few months. Additional males probably have come from more than the 23 nests we found in the study area. The flying range of the workers of the large *Melipona fasciata* Latreille was 2.1–2.5 km (Roubik & Aluja, 1983) and of the small *T. minangkabau* (Sakagami & Inoue) was less than 0.5 km (Inoue *et al*., 1985), hence that of *T. laeviceps*, somewhat larger than the latter, must be somewhere in between the two. But the flying range of males is assumed to be several times that of workers which, unlike the males, have to return to their nests each time with the collected forage.

Fourth, we are not aware of reports of swarms with mixed male species, except Velthuis *et al*. (2005) who mention the possibility of such an occurrence. We found that 1.4% of the males sampled on 5 May were *L. terminata* and *Li. furva*, but mixed male swarms had been observed previously in other Asian stingless bees (Bänziger, unpubl. data), *e.g*., near Chaiprakan, Chiang Mai — at a nest of *Li. furva*: *Li. furva*, *T. laeviceps*, and *T. fuscobalteata* on 25 June 2009; and three cases at nests of *L. terminata*: *L. terminata* and *T. laeviceps* on 20 March 2010; *L. terminata*, *T. laeviceps*, *T. fuscobalteata*, and *T. testaceitarsis* (Cameron) on 6 June 2010; and *L. terminata*, *T. laeviceps*, *T. testaceitarsis*, and *L. doipaensis* (Schwarz) on 11 April 2011. In the latter case the number of males was recorded: among 199 males of *L. terminata* the heterospecifics were 2, 5, and 5, respectively, thus a total of 6%. Explanation for the last three cases might be the vicinity of these species' nests in limestone rock faces (Bänziger *et al*., 2011) so that they might have been visually attracted by the swarms while accidentally flying nearby. In addition, Galindo López & Kraus (2009) showed that congregating males have an odor which is attractive to other males, although it is not known whether this is attractive to heterospecifics. On the other hand, in our study of *T. laeviceps*, *L. terminata* were seen circling persistently around the nest entrance on several days (*L. terminata* is readily discernible by its much larger size). Whereas it is quite possible that such males instinctively fly to the head of the swarm which tends to be near the nest entrance, and additionally may be visually attracted to it, it is also possible that *L. terminata* were attracted by an odor emanating from the nest of *T. laeviceps*, such as that produced by cephalic glands of virgin queens of *S. mexicana* (Verdugo-Dardon *et al*., 2011). Engels *et al*. (1997) showed that the sex pheromone from the cephalic glands of virgin queens of *S. postica* (Latreille) consists of multicomponent mixtures and that these attract males at a long or short range. We propose that the potent, highly volatile long-range mixture may be attractive to some degree also to heterospecific males, whereas the less volatile short-range mixture inducing copulation (Engels *et al*., 1997) is species-specific, hence precluding heterospecific mating.

Identification of our *T. laeviceps* follows Rasmussen & Michener (2010). Interestingly, molecular analyses of our samples (Bänziger & Khamyotchai, pers. obs.) ranging from northern Thailand to near the tip of Peninsular Malaysia, suggest the existence of at least seven cryptic species under this name. However, molecular analysis of one worker from the study nest and four males swarming there, as well as of workers of 15 other nests of *T. laeviceps* sampled from Chiang Mai town and wider neighborhoods showed that they belong to the same taxon.

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