

Nuptial flight of the Southeast Asian plant-ant *Crematogaster captiosa* (Forel, 1911) and the phenology of colony founding

BRIGITTE FIALA^{1*}, ROSLI BIN HASHIM², KLAUS DUMPERT³
AND ULRICH MASCHWITZ⁴

¹University of Würzburg, Animal Ecology and Tropical Biology, Biocenter,
Am Hubland, 97074 Würzburg, Germany

²Institute of Biological Sciences, Faculty of Science Building, University of
Malaya, 50603 Kuala Lumpur, Malaysia

³Im Maierbrühl 59, 70112 Freiburg, Germany

⁴Fachbereich Biowissenschaften, Johann-Wolfgang-Goethe-Universität Frank-
furt, present address: Anemonenweg 33, 63263 Neu-Isenburg, Germany.

*Corresponding author: fiala@biozentrum.uni-wuerzburg.de

ABSTRACT. Despite the great importance of nuptial flights for ants, little is known about the swarming processes from the highly diverse tropical regions, especially rainforests. This is particularly true for ants living in obligate symbiosis with myrmecophytic plants. Here we present the first direct observations of the swarming event in the association between *Crematogaster captiosa* and the pioneer tree *Macaranga bancana* in Southeast Asia. Nuptial flights of *C. captiosa* on *M. bancana* took place during the night, and alate females were seen to copulate with alate males on the tree. Data on *C. captiosa* from the Malay Peninsula as well as Borneo indicate that sexual production and colony founding occurs throughout the year. Despite episodic fruiting seasons of the host plants, *Macaranga* saplings for colony founding can also become available outside peak seasons from seed banks after disturbance. Therefore, continuous swarming might be a good strategy to avoid strong competition for limited nesting sites while still securing permanent colonisation of saplings - a prerequisite for their survival.

Keywords: Ant-plant, alate production, mating, *Macaranga*, myrmecophytes, swarming, reproduction

INTRODUCTION

Though being a central event in the life cycle of ants, astonishingly little is known about their reproductive ecology. Dispersal and new colony foundation are mostly conducted by winged young queens mating with males during so-called nuptial flights, often in a massive, highly synchronized swarming. Most data on nuptial flights refer to temperate zones (summarized

e.g., in Hölldober & Wilson 1990; Dunn et al. 2007; Noordijk et al. 2008) and only few reports have come from the tropical perhumid forests which harbor the highest diversity in ants. Information about patterns of reproductive processes and swarming behaviour of tropical ants are scattered and hidden in the literature. Detailed observations have mainly been published of army ants (Gotwald 1995; Nascimento et al. 2011) and neotropical leaf cutter ants (e.g Baer & Booms-

ma 2006; Staab & Kleinadam 2014), invasive *Solenopsis* (e.g. Markin & Dillier 1971; Wuellner 2000), the Southeast Asian *Camponotus gigas* (LATREILLE, 1802) (Pfeiffer & Linsenmair 1997) and recently from *Oecophylla smaragdina* (FABRICIUS, 1775) in northern Australia (NIELSEN et al. 2016). Some reports (mainly from the Neotropics) deal predominantly with flight phenology (e.g., Kaspari et al. 2001a, b; Torres et al. 2001; Feitosa et al. 2016), and revealed that the reproductive season of tropical ant species can vary from highly synchronous to nearly continuous throughout the year. In aseasonal perhumid tropical forests where the climate imposes no direct constraints on mating, the dispersal timing of queens may be related to the changing availability of nesting sites.

A conspicuous feature of many tropical habitats are ant-plants (myrmecophytes) which provide nesting space in hollow plant structures for specific plant-ant associates which exclusively live inside these plants, and defend them against herbivore damage and climbing plants (reviewed e.g., in Heil & McKey 2003; Rico-Gray & Oliveira 2007). The reproductive phenology of plant-ants may depend on the host plants' reproductive phenology as the host plants provide new saplings for colonisation. Plant-ants should be strongly dependent on the spatial and temporal distribution of saplings, and two Neotropical species (*Allomerus octoarticulatus demerarae* (Wheeler, 1935) and *Pheidole minutula* (Mayr, 1878), were indeed reported to show a seasonal pattern of colony founding in their host plants (Vasconcelos 1993; Fonseca 1999; Frederickson 2006). However, with the exception of an early study on the *Pseudomyrmex-Acacia* (now *Vachellia*)-association in Central America (Janzen 1967), information on nuptial flights in obligate ant-plant symbioses is lacking.

For more than three decades we have been studying one of the most diverse obligate ant-plant symbioses worldwide: the association between trees of the genus *Macaranga* Thouars, 1806 (Euphorbiaceae) and ants of the genus *Crematogaster* Lund, 1931 (*C. borneensis-group*) (or –rarely –*Camponotus*) species in Southeast Asia. This very complex system consists of six groups of organisms (recent overview e.g., Fiala et al. 2011, Maschwitz et al. 2016). All *Macaranga*-

ant associations begin with newly mated foundress queens searching for a suitable host plant sapling for colonisation. Sexuals are produced inside the plants when the host trees are often already taller than 4 m, making direct observations on reproduction extremely difficult. Despite extensive field work on the system, we had never seen alates leaving their host tree before the present study. We here now describe the first direct observations of the swarming event in the association between *M. bancana* (Miq.) Müll. Arg., 1866, and *C. captiosa* Forel, 1911. We provide further information on the reproductive process such as the production of ant alates and the temporal patterns of colony foundation through the year. We aim to contribute to an important life history strategy feature of the extremely specialized plant-associated ants, and discuss whether this tight association with a host plant may shape their reproductive ecology.

MATERIAL AND METHODS

Study Species

The plants. The pioneer tree species *Macaranga bancana*, sect. *Pachystemon*, (formerly known as *M. triloba* (Thunb.) Müll.Arg., 1866 (Davies 2001)) occurs in in lowland areas of dipterocarp forests as a comparatively small subcanopy species (see Fig. 1) up to 23m height. Like most myrmecophytic *Macaranga* trees, *M. bancana* has episodic annual reproduction (Davies and Ashton 1999; Moog et al. 2002, Fiala et al. 2011), and the peak availability of young domatia-bearing saplings is mainly following this reproductive cycle. However, seedlings can also arise from seed banks after forest disturbance (Howett & Davidson 2003). The *M. bancana* population in our main study site, Ulu Gombak, flowers mainly from January until April, with varying intensity over the years, and a few plants were also seen flowering in June-August and in November. Fruit set occurred usually three to four months after flowering. In open areas, often dozens of seedlings could be found directly underneath mother trees, but mortality was high.



Fig. 1. Upper row: Habitat of *M. bancana* trees (white arrow, with trilobed leaves), middle row left: stem full with large larvae and pupae and alate females of *C. captiosa*, right: opened stem of *M. winkleri*, alate female of *C. sp. 8*. (photo E. Linsenmair); lower row (left to right): colonisation of *M. bancana* by *C. captiosa* at nighttime; colonising queen of *C. sp. 8* on *M. winkleri* at daytime (photo E. Linsenmair); colonising queen of *C. linsenmairi* on *M. pearsonii*, plant pith from the interior which is later used to seal the entrance hole is visible on the stem surface.

The ants. The ants associated with different *Macaranga* species comprise ten *Crematogaster* species, nine of belonging to the closely related *C. borneensis*-group (further information Feldhaar et al. 2016). After localization of a host-plant, single queens enter a sapling by chewing an entrance hole into an internode (Fig. 1). The hole is sealed from the inside and colony founding is claustral. The first workers open up the internodes and start foraging for food bodies produced by the plant as well as for honeydew from specific coccids (Fiala & Maschwitz 1990; Heckroth et al. 1998, Ueda et al. 2008). Whereas several colonies may be founded simultaneously in different internodes, only a single monogynous colony finally inhabits each host (Fiala & Maschwitz 1990; Feldhaar et al. 2003). The only fertile physogastric queen of the colony is always situated in a low region of the stem, so all female alates found elsewhere in the tree are newly produced. Alate production of our study species *C. captiosa* (provisionally named *Crematogaster* msp. 4 in our earlier publications) begins in colonies containing 5000 or more workers (Feldhaar et al. 2003). *Crematogaster captiosa* is a very widespread species occurring in Peninsula Malaysia, southern Thailand, Sumatra, and Borneo.

Study sites

(1) **Behavioural observations on swarming** were conducted near the Ulu Gombak Field Studies Centre (FSC) of the University of Malaya, Malay Peninsula, 30 km from Kuala Lumpur (N 03°19.111'; E 101°45.912', 220 a.s.l.). The FSC is surrounded by secondary dipterocarp forest where ant-inhabited trees of *M. bancana* are very common along roadsides. The climate is aseasonal with an average temperature in of 27.1 °C (Climate-data.org 2016).

(2) **Data on presence of colony founding queens and sexuals** of *C. captiosa* were collected on the Malay Peninsula and in Borneo. Our main study site in Borneo was at Poring, Kinabalu Park, Sabah, (including forest reserves at Bukit Taviu, Deramakot, and Danum Valley). Further primary and secondary forest sites were visited several times in Sarawak (e.g., Lambir, Mulu, Kubah) and Brunei (Belalong, and Labi Road).

Direct observation of the swarming process.

We collected data on alate swarming behaviour in Ulu Gombak during three field stays in December to May in 2012- 2014. Trees containing alates are usually too tall for direct observations. We finally managed to cautiously bend down the crowns of four trees (about 5-6 m, dbh < 8 cm) which grew on the base of a steep step-like slope. This position was suitable for viewing the swarming holes while standing on ladders or plastic chairs. The tree providing the best observation position was selected as the main study tree, which was then checked at different times of the day and later observed for several hours from sunset on for ten nights (27 February to 8 March 2013). Due to the distance to the three other trees, and the difficult habitat conditions in the dark, these could not be observed simultaneously. As light disturbed the swarming, we had to use torches covered by red glass for our observations. For one day we had access to a Sony Cam recorder, HDR-SR8E, which allowed to record in the infrared range, however, due to technical problems we could only record the start of the swarming process.

Distribution of alates within the colony (Ulu Gombak).

Whereas the males of *Macaranga*-associated *Crematogaster* are small and can use the entrance holes of the workers to leave the plant, the females are much bigger (Fig. 2). To find out where exactly female alates leave the plants, we felled eight *M. bancana* trees in April 2013, checked them for presence of larger holes, and measured their diameter and height. To investigate an example of the positions of sexuals in the plants, three trees were opened completely.

Monitoring of ant sexuals and colonising queens in Ulu Gombak.

During three field stays from December to May 2012- 2014, six trees were opened every month and checked for sexual brood and alates. In addition, monitoring was continued once per month from May to December 2013 (by RH), thereby allowing us to cover a year-long period. In all study periods *Macaranga* saplings were inspected for new colony foundations once to twice per month by searching for plants with freshly excavated entrance holes. At least five of these plants were opened to check for queens (still without brood or workers). Recent



Fig. 2. View into an opened stem of *M. bancana*. Visible are workers, males and female alates of *C. captiosa* (photos Muhammad Rasul Abdullah).

colonisations can easily be differentiated from older entrance holes, as they are loosely sealed with a bright plug made of pith (Fig. 1) from the plant interior while entrances are closed by darker callus growth after a few weeks.

Presence of sexuals and colonising queens in other regions. During the decades of our research many different *Macaranga-Crematogaster* associations were checked for presence of alates and new colonisations (mainly by BF with additional data from UM and occasionally other colleagues). We here present data from field work mainly in Borneo from 1991 on. At each study site, we opened at least five recently colonised saplings per *Macaranga* species at the beginning and at the end of our stays. We noted presence of colonising queens and other colony stages (colonies with brood and workers). We also tried to find at least two accessible larger trees per species

at each site to check for alates or alate brood by either cutting open branches or, if possible, felling whole trees. In this study only information on *C. captiosa* will be provided.

RESULTS

Swarming frequency and time. We observed nuptial flights of *C. captiosa* in detail from 27 February to 8 March 2013. All swarming took place after sunset. The colony on our main study tree swarmed on each of the first three nights, then stopped for two nights. After swarming on day six, day seven remained without swarming. The next three days the colony swarmed again. The four colonies under observation were not always seen swarming on the same days, but parallel swarming of two colonies occurred. We could not relate swarming to any weather event (before

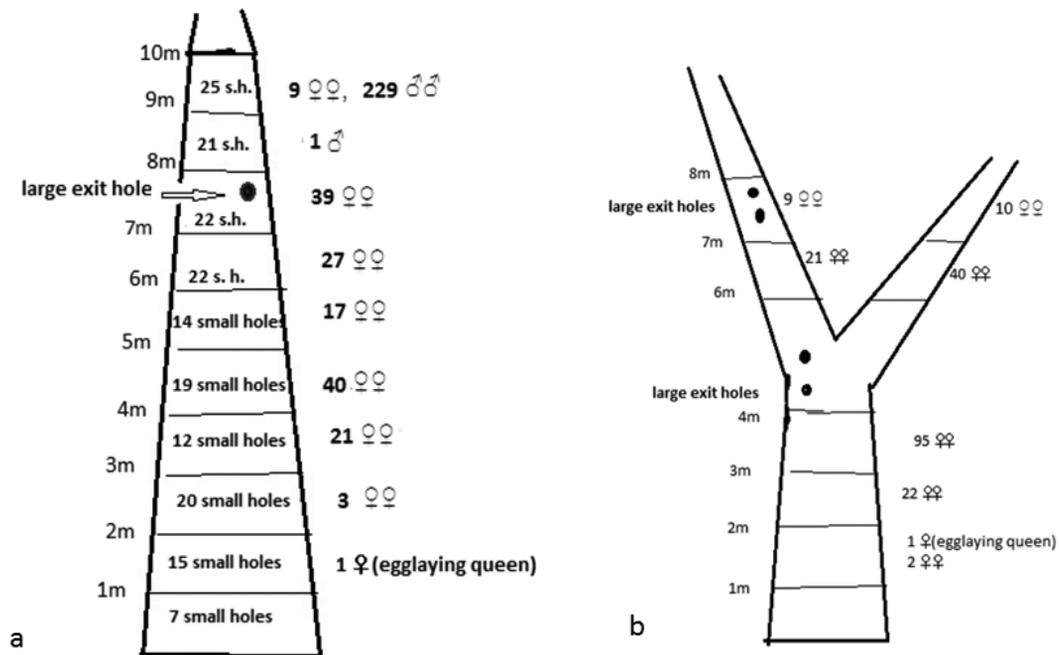


Fig. 3. Sketches of two examples of the distribution of alates of *C. captiosa* in *M. bancana* (April 2013). a) Tree of 10.2 m with one thick and 8 thin branches (not shown). Only one large exit hole for alates at 6.43 m at a tree diameter of 5.5m. The tree contained one physogastric queen, 192 winged females and 290 males. 50 males and 35 females were located in the branches, the rest in the stem at various heights. Males were found mainly in the upper parts of the stem. s.h. = number of small worker holes/m stem. b) Tree of 8.50 m with two thick and 6 small branches (not shown). Four exit holes at 4.1m, 4.4 m, 7.5 m, 7.7 m. Only the upper ones were used for swarming during our observations. This colony contained only 199 female alates, no males.

and on the swarming days it was dry or rain had occurred). Rain during the swarming stopped the flights. We observed alates flying out of our study trees a further 20 times when randomly passing our study trees (8 March until end of April 2013). Anecdotal observations were made during this same period of single *C. captiosa* female alates attracted to lamps at FSC and light traps for catching other insects (approximately 30 times in total).

Swarming behaviour. The general process was similar in all swarming events. We describe one example in more detail here. Before alates came out from the nest, an increasing number of workers appeared at the stem surface where they remained present until the end of swarming. At about 7 p.m. (after dusk) the first males came out. They left the nest through the large female swarming holes at about 6 m height (see Electronic Supplementary Material Fig. S1-S4) as well as through small worker exits close by, and began to fly off. At this time it was already dark to the human eye. On average ten minutes later, the females came out in increasing numbers. They moved in an excited way between workers and the males which ignored them. Usually the females did not start to fly away immediately but before takeoff moved up to 8 cm away from the swarming hole (see Electronic Supplementary Material Fig. S1-S4). Whereas the males coming out of the interior were not contacting the young females of their own colony before departing, we did observe six copulations directly near to the swarming hole: flying males landed close to the hole, contacted females there and immediately copulated with them *a tergo*. Most of the swarming females departed in the course of the next 1.5 hours with a maximum number of ten visible females at 19 lux. These females instantly took off. Due to the surrounding darkness, we could not follow the course of their flight. Some alates also moved back into the nest. We estimate that less than 50 alates flew off per swarming event. At the end of the main swarming period, workers increasingly began to hold still active alates by their antennae and legs on the surface and thus actively prevented any delayed swarming. Some days, only a few males and/or females came onto the surface, stayed on the branch for a short while

and then went back into the stem. Sometimes females just looked out of the exist hole but did not come out at all.

Alate distribution in the tree interior. Both females and males were found in 37 of the 54 *M. bancana* trees in Ulu Gombak that we had felled and cut open completely over the study period (Fig. 3a), but 16 colonies produced only females (Fig. 3b) and one colony was found only with males. In the latter case we could not find the original queen low in the trunk but found three (probably secondary) egg-laying queens in different internodes at a higher position of the stem. We found two types of entrance holes on the *Macaranga* trees. Besides the many small holes used by the workers, we always discovered bigger holes obviously used as swarming exits. The number of swarming exits ranged from one to five per tree (Table 2, Fig. 3a,b). The smallest of the 13 swarming holes on all trees was 1.9 x 1.9 mm, the largest 4.1 x 6 mm (mean width: 2.52 ± 0.6 mm, mean height 3.6 ± 2.3 mm). Worker holes were always much smaller (mean horizontal and vertical diameter 1.02 ± 0.1 and 1.93 ± 0.8 mm, respectively, n = 20), and were usually distributed from the branches to the trunk base of the tree (Fig. 3a,b). The tallest of these trees had 105 worker entrance holes on its main stem. About 30 % of them were permanently used, whereas 70 % (mainly in the lower parts) were camouflaged with particles at the entrance. Entrance holes used by alates were mostly found in higher positions of the main stem (Fig. 3) or less frequently on the base of large branches. When opening a tree, the majority of the alates were distributed in the upper region of the tree, in the trunk and in thick branch regions (examples Fig. 3a, b). In the upper parts of the tree males were found, in the middle of the tree males and females occurred together, while in the lower parts of the stem mainly females were present, often with female brood and workers (see examples Fig. 3a, b). In the third tree of 6.3 m height (not shown) the distribution was similar but there were so many males in the upper parts of the stem that we did not count them. We counted 144 female alates mainly in the trunk from 2m height up to the top. The much smaller males were also found in more peripheral thinner branch regions. We found alates on *M. bancana*

in trees of at least 3 m - 4 m height. Ten younger trees (2- 4 m) which had no large holes also did not contain alates.

Phenology of alate production and colony founding

Ulu Gombak. Winged females and males as well as female larvae and pupa (Fig. 1) were present in *M. bancana* trees from December 2012 to December 2013. At least five freshly colonised saplings of *M. bancana* containing *C. captiosa* queens (without brood or workers) were found in all months, also indicating continuous presence of dispersing females during that time. Newly colonised saplings and sexual brood and adults were also found during our two further study periods in December to April 2012 and 2014 (Table 1, bottom rows).

Other regions. In Peninsula Malaysia *C. captiosa* occurred mainly in *M. bancana* (and in *M. hullletti* at lower elevation), in Borneo it was found additionally in endemic species, in Sarawak and Brunei (NW-Borneo) mainly in *M. trachyphylla*, but also on *M. calcicola*, *M. lamellata*, *M. umbrosa*, and the non-waxy form of *M. aetheadenia*; in our main study area in Sabah (NE-Borneo) it was most abundant on *M. indistincta* and *M. glandibracteolata*, and also occurred on *M. angulata* and the rare montane species *M. petanostyla*. Our checks of different *Macaranga-Crematogaster* associations from 1991-2008 showed that there was no field stay without coming across newly

colonised saplings indicating recent swarming of queens. (All older colony stages (queens with egg, larvae, pupae and workers) were also present.) Sexual brood, and alates were also found at different times of the year (Table 1). We tried to open at least two trees per study period but systematic data collection was not always possible, as we for instance could not conduct destructive sampling in national parks. Even if we did not find alates in opened branches, they could have been present in the stem interior where we could not reach them (thus possible presence is marked with a '?' in Table 1).

We could also obtain two random observations of *C. captiosa* queens while excavating an entrance hole into a sapling of *M. indistincta* (9:15h, 14 August 1991, 10:00 h, 2 September 2006, Poring, Sabah). Further observations were also randomly made of other species: *C. linsenmairi* Feldhaar, 2016, on *M. aetheadenia* (22:00 h, 25 August 1996 Sibu, Sarawak) and *M. pearsonii* (Fig.1) (10:45 h, 12 April 2000, Deramakot), as well as *C. decamera* Forel, 1910, on *M. hypoleuca* (9:00 h (8 August 2004), Poring; 10:15 h, 11:00 h, 11:30 h, (10 April 2000) Deramakot). *Crematogaster decamera* was also found in the afternoon on *M. hypoleuca* (13:30 h, 17 May 2006, Danum Valley), and *M. motleyana* (14:00 h, 5 April 2000, Deramakot). Queens of the yet undescribed *C. sp. 8* were found excavating a hole in *M. winkleri* (Fig.1) (11:20, April 1998) and around 14:00 h (16 May 1997 and 8 August 2004, Poring).

Table 2. Number and position of swarming holes in eight trees of *M. bancana* in Ulu Gombak, Malay Peninsula, April 2013. Included is total tree height, number of swarming holes (those at least 1.9 x1.9 mm; see main text) and height of each swarming hole above the ground.

Tree height (m)	No. of swarming holes	Height of swarming holes (m)
5.8	5	2.70, 3.25, 4.75, 4.92, 6.16
6.2	2	5.1, 5.7
6.3	2	4.57, 5.32
6.9	1	6.16
8.2	4	3.10, 5.55, 6.80, 7.40
8.45	1	4.65
8.5	4	4.10, 4.40, 7.55, 7.75
10.2	1	6.43

Table 1. Colony founding queens and sexual stages of *C. captiosa* (male alates, and female brood and alates) in different regions during different study periods.

Study period.	SABAH				SARAWAK, BRUNEI				PEN MAL			
	ang, gla, ind, pet				aet, ban, cal, hul, lam, tra, um				ban, hul			
	cq	♂	♀-br.	♀-al.	cq	♂	♀-br.	♀-al.	cq	♂	♀-br.	♀-al.
20.12.84-22.02.85									X	X	X	X
18.12.85-20.03.86									X	X	X	X
27.12.86-25.03.87									X	X	X	X
28.10.88-04.12.88									X	X	X	X
07.12.89-21.01.90												
29.07.91-21.09.91	X	?	?	?								
14.02.92-22.02.92	X	?	?	?								
01.03.92-30.03.92					X	?	?	?	X	?	?	?
28.10.92-27.12.92	X	?	?	?	X	X	X	X	X	?	?	?
06.01.94-20.03.94	X	?	?	?	X	?	?	?	X	?	?	?
18.10.94-21.11.94	X	?	?	?								
28.01.95-14.02.95	X	?	?	?								
09.08.95-30.08.95	X	?	?	?	X	?	X	X				
30.08.95-14.09.95									X	?	?	?
06.04.96-23.05.96	X	X	X	X	X	?	?	?				
12.08.96-28.08.96	X	?	X	X	X	X	?	?	X	?	?	?
31.03.97-23.04.97	X	?	?	X								
23.03.98-18.04.98	X	X	X	X								
170.2.99-26.03.99	X	?	?	X	X	?	X	X				
13.03.00-04.04.00	X	X	X	X	X	?	?	?	X	X	X	X
11.08.00-08.11.00	X	?	X	X					X	X	X	X
01.04.01-21.04.01	X	X	X	X								
15.09.01-15.11.01	X	?	?	?								
09.03.02-04.04.02	X	?	?	?								
27.08.03-07.09.03	X	?	?	?								
03.07.04-21.08.04	X	?	?	?								
06.08.05-11.09.05	X	X	?	?	X	?	?	?				
09.03.06-29.03.06	X	?	?	?								
07.08.06-05.09.06	X	X	X	?	X	?	?	?				
20.08.07-16.09.07	X	?	?	?	X	?	?	?				
18.08.08-11.09.08	X	?	?	?	X	?	?	?				
01.12.12-16.04.12									X	X	X	X
14.12.13-08.12.13									X	X	X	X
17.12.14-18.04.14									X	X	X	X

Cp= Colony founding queens in young saplings, ♂ = winged males, ♀-br.= brood (larvae and pupae), ♀-al.= winged females. X = At least 5 saplings per species contained colony founding queens (still without brood) at the beginning and the end of the study period. ? = not found in branches of two trees but perhaps nevertheless present in the stem (further information see text). Grey shading: No data collection in this region during the respective study period.

Abbreviations of *Macaranga* species: ang= *angulata*, gla= *glandibracteolata*, ind= *indistincta*, pet = *petanostyla*, aet= *aetheadenia*, ban = *bancana*, cal= *calcicola*, hul= *hulleitii*, lam= *lamellata*, tra = *trachyphylla*, um= *umbrosa*. Sites in Sabah mainly comprise: Kinabalu Park, Poring, Bukit Taviu, Deramakot, Danum Valley. Sarawak: Forest near Lambir, Mulu, Sibul and Kubah, Brunei: Belalong and Labi Road. Pen Mal: Ulu Gombak, Kepong, Genting Highlands, Fraser's Hills, Pasoh.

DISCUSSION

Reproductive phenology and behavior of obligate plant-ants associated with tall host trees is difficult to study. To our knowledge, our study provides first direct observation of the swarming behaviour of plant-ants in tropical rainforests. We show that nuptial flights of *C. captiosa* on *M. bancana* took place during the night and we suggest that males and females might use the host plants as a meeting place.

The swarming process

As we have observed copulations of *M. captiosa* on the *Macaranga* tree, this could indeed be a good mating place in the dark dense forests. We did not see copulations between males and females leaving the same holes on the tree and suppose that the males of *C. captiosa* came from other colonies close by. In many ant species the alates fly to landmarks standing well above the surrounding vegetation such as solitary trees, poles, etc. and copulation may often take place in the air (Hölldobler and Wilson 1990). In the original habitats of *Macaranga*, trees are rather isolated, so random meeting in the midst of a very diverse and much taller plant matrix could be difficult. Swarming events have rarely been observed in tropical forests (e.g., Pfeiffer & Linsenmair 1997), and most records come from open habitats (e.g. Gotwald 1995; Staab & Kleineidam 2014; Nielsen et al. 2016). In the only direct observation of a plant-ant swarming we are aware of, Janzen (1967) described that alates of *Pseudomyrmex* met at higher objects in the open savanna landscape, and that females attracted males by conspicuous lifts of the gaster upwards to release scents, a behaviour that was not observed in *C. captiosa*.

Massive swarming flights perhaps occur due to the high predation risks during mating and dispersal of queens and/or to maximize mating success (Hölldobler & Wilson 1990; Peters & Molet 2010). The advantage of year-long mating may come with the disadvantage of lower abundance of alates per swarming flight, requiring some common flight triggers (Torres et al. 2001). We did not find strict synchronization among our four directly observed study trees of *M. bancana*. Weather conditions, like rain, have been found

to play a role in the timing of swarming events (Hölldobler & Wilson 1990). However, rain during the flight stopped the swarming of *C. captiosa* (but not in other night swarming ants at the Ulu Gombak study site, pers. obs.). Also, *Camponotus gigas* was reported to fly in light rain but heavy rain could prevent the alates from taking off (Pfeiffer & Linsenmair 1997).

Swarming of *C. captiosa* in Ulu Gombak took place in the first hours of darkness and we never came across swarming during daylight. The nuptial flight is directly linked with dispersal and colony founding. We came across most of the colonising queen ants of *C. captiosa* on *M. bancana* in the early morning (see also Fiala & Maschwitz 1990). For *Macaranga*-associated ants there are indications for the use of olfactory host recognition (Inui et al. 2001, Jürgens et al. 2006; and unpubl. research) making night searches possible. We do not know how long queens have to search for the small *Macaranga* saplings in the midst of other vegetation in the dark forests. Once a tree is found, it can take up to several hours to excavate an entrance hole into the internode (Fiala et al. 1990; Federle et al. 1998; and unpubl. obs.), therefore many queens are still found excavating during the day. Queens might also rest after mating before they fly out again and search for a nesting site as recorded for *O. smaragdina* (Nielsen et al. 2016).

Night swarming can be interpreted as an avoidance strategy against day active predators like birds or lizards, but night active predators also exist (e.g. bats were reported to feed on *Camponotus gigas* swarms (Pfeiffer & Linsenmair 1997). Nocturnal mating and dispersal flights nevertheless does not seem to be the rule among plant-ants. *Pseudomyrmex ferrugineus* species swarmed and copulated late at night and early in the morning (Janzen 1967), and most *Azteca* queens colonised during the hot midday (Yu & Davidson 1997). Furthermore, in the Southeast Asian plant-ant genus *Cladomyrma*, colony founding queens were seen during day time (Maschwitz et al. 1991, Eguchi & Bui 2006).

Production of sexuals

Although we could not cover entire years in our field stays (with the exception of 2013), we usually found sexuals of *C. captiosa* at dif-

ferent times of the year. In most cases females and males alates occurred together on one tree but in a few cases only males or females were present. This pattern was also reported in other *Macaranga* species (Feldhaar et al. 2003), and known from other plant-ants (e.g., Janzen 1967; Longino 1991; Gaume & McKey 2002, but for instance in *Allomerus octoarticulatus* a strongly split sex ratio was exhibited (Frederickson & Gordon 2009)).

We also came across all developmental stages of colonies, freshly colonising queens as well brood and different numbers of workers during our study periods (see also detailed results on proportion of colony stages of *C. captiosa* in Fiala & Maschwitz 1990). As colony development from founding to emergence of first workers takes about 4 weeks, colony founding events must have taken place at least 4-8 weeks before, narrowing the time window without direct evidence on sexual production (for example: last check 14 April 2000, first check again 11 September, therefore indicating a colonisation (=swarming event) at the beginning of July at the latest, for colonies with several dozens or hundreds of workers). Further support for continuous colony founding comes from our data on other *Macaranga*-associated ant species (e.g., Federle et al. 1998 for *M. pruinosa*, Türke et al. 2010 for *M. hypoleuca*) as well as a long-term study of three *Macaranga* species in Lambir National Park (Murase et al. 2002). Reproductive processes are not well known from other plant-ant systems (summarized in Fiala et al. 2014). A few plant-ants seem to synchronize their yearly reproduction pattern to the peak availability of new host plants (Vasconcelos 1993, Fonseca 1999; Frederickson 2006), whereas *P. ferrugineus* reproduced continuously throughout the year (Janzen 1967).

Although we found continuous colonisation in *Macaranga*, we cannot exclude that relative colonisation frequency might also vary over the year. *Macaranga* saplings provide spatial as well as temporal patchiness of nesting sites. The abundance of plant hosts poses the upper limit to the abundance of colonies. The presence of multiple foundress queens within *Macaranga* seedlings (e.g. Fiala et al. 1999, Murase et al. 2002, Türke et al. 2010) shows very intense local competition for newly available nesting

space. Seedlings are rare in gaps of primary forests, but reach high density in disturbed forests (e.g., Türke et al. 2010, further own obs.). Seeds of the pioneer tree species can remain viable in the soil seed bank (e.g., Howell & Davidson 2003). As timing of disturbances and seed germination is random with respect to fruiting phenology, unpredictable spatial and temporal variation of saplings results, especially in primary forests which have few natural disturbances. Therefore, tight synchronization of plant and ant reproductive peaks appears unlikely.

CONCLUSION

Rare but massive and seasonally synchronized swarming of many queens would lead to a shortage of available nesting sites (i.e., saplings at a given time). Therefore, frequent swarming of rather few females might be the best strategy, benefitting both plants and ants in the association. Strong competition for nesting sites is avoided but colonisation of most saplings arising after disturbance is secured - a prerequisite for their survival (Fiala et al. 1989; Heil et al. 2001). Nowadays, extensive even-aged stands of *Macaranga* trees in secondary forest and logged sites exist, probably leading to a high local abundance of alates and saplings, and changing distances of dispersal - with unknown future consequences for these associations.

ACKNOWLEDGMENTS

Permission to conduct research in Malaysia over the last decades was kindly granted by the Economic Planning Unit (EPU), Kuala Lumpur and Kota Kinabalu, Sabah. We thank Sabah Parks, Kota Kinabalu, especially Dr. Jamili Nais and Dr. Maklarin bin Lakim, for long-term support. BF is grateful for permits from the Danum Valley Management Committee, the Forest Department, Sarawak, Universiti Brunei Darussalam and Brunei Museum. Eduard Linsenmair and Muhammad Rasul Abdullah Halim kindly provided photographs. We thank Armin Jakob, Hans-Peter Heckroth, Daniela Guicking, Heike Feldhaar, Achim Moog and Ute Meyer for infor-

mation. German Research Foundation (DFG) is acknowledged for financial support of some of our earlier projects. We thank the editors, Adam Cronin and Martin Pfeiffer, as well as two anonymous referees for valuable comments which greatly improved the manuscript.

REFERENCES

- Baer B and Boomsma JJ, 2006. Mating biology of the leaf-cutting ants *Atta colombica* and *A. cephalotes*. *Journal of Morphology* 267: 1165-1171.
- Climate-data.org. (2016) <https://en.climate-data.org/location/25985/>. Accessed 23 December 2016
- Davies SJ and Ashton PS, 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. *American Journal of Botany* 86: 1786-1795.
- Davies, SJ, 2001. Systematics of *Macaranga* sects. *Pachystemon* and *Pruinosae* (Euphorbiaceae). *Harvard Papers in Botany* 6: 371-448
- Dunn RR, Parker CR, Geraghty M and Sanders NJ, 2007. Reproductive phenologies in a diverse temperate ant fauna. *Ecological Entomology* 32: 135-142.
- Eguchi K and Bui TV, 2007. Ecological notes on a plant-ant *Cladomyrma scopulosa* Eguchi & Bui (Hymenoptera, Formicidae, Formicinae) associating with a tree species *Saraca dives* (Leguminosae). *Asian Myrmecology* 1: 51 – 58.
- Federle W, Fiala B and Maschwitz U, 1998. *Camponotus (Colobopsis)* (Mayr 1861) and *Macaranga* (Thouars 1806): a specific two-partner ant-plant system from Malaysia. *Tropical Zoology* 11: 83-94.
- Feitosa RM, da Silva RR and Aguiar AP, 2016. Diurnal flight periodicity of a Neotropical ant assemblage (Hymenoptera, Formicidae) in the Atlantic Forest. *Revista Brasileira De Entomologia* 60: 241-247.
- Feldhaar H, Fiala B, Hashim R and Maschwitz U, 2003. Patterns of the *Crematogaster-Macaranga* association: The ant partner makes the difference. *Insectes Sociaux* 50: 9-19.
- Feldhaar H, Maschwitz U and Fiala B, 2016. Taxonomic revision of the obligate plant-ants of the genus *Crematogaster* (Lund) (Hymenoptera, Formicidae, Myrmicinae), associated with *Macaranga* (Thouars) (Euphorbiaceae) on Borneo and the Malay Peninsula. *Sociobiology* 63 : 651-681.
- Fiala B, Maschwitz U, Tho YP and Helbig AJ, 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* 79: 463-470.
- Fiala B and Maschwitz U, 1990. Studies on the South East Asian ant-plant association *Crematogaster borneensis/Macaranga*: Adaptations of the ant partner. *Insectes Sociaux* 37: 212-231.
- Fiala B, Jakob A and Maschwitz U, 1999. Diversity, evolutionary specialization and geographic distribution of a mutualistic ant-plant complex: *Macaranga* and *Crematogaster* in South East Asia. *Biological Journal of the Linnean Society* 66: 305-331.
- Fiala B, Meyer U, Hashim R and Maschwitz U, 2011. Pollination systems in pioneer trees of the genus *Macaranga* (Euphorbiaceae) in Malaysian rainforests. *Biological Journal of the Linnean Society* 103: 935-953.
- Fiala B, Meyer U, Hashim R and Maschwitz U, 2014. Temporary sterilization behavior of mutualistic partner ants in a Southeast Asian myrmecophyte. *Ecological Research* 29: 815-822.
- Fonseca CR, 1999. Amazonian ant-plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology* 15: 807-825.
- Frederickson ME, 2006. The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia* 149(3): 418-427.
- Frederickson ME and Gordon DM, 2009. The intertwined population biology of two Amazonian myrmecophytes and their symbiotic ants. *Ecology* 90: 1595-1607.
- Gaume L and McKey D, 2002. How identity of the homopteran trophobiont affects sex allocation in a symbiotic plant-ant: the proximate role of food. *Behavioral Ecology and Sociobiology* 51: 197-205.
- Gotwald WH, 1995. The army ants: The biology of social predation. Cornell University Press, Ithaka, New York, 302 pp.
- Heckroth H, Fiala B, Gullan P, Idris A and Maschwitz U, 1998. The soft scale (Coccidae) associates of Malaysian ant-plants. *Journal of Tropical Ecology* 14: 427-443.
- Heil M, Fiala B, Maschwitz U and Linsenmair KE, 2001. On benefits of indirect defence: short- and long-term studies of antiherbivore protection via mutualistic ants. *Oecologia* 126: 395-403.

- Heil M and McKey D, 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology Evolution and Systematics* 34: 425-453.
- Hölldobler B and Wilson EO (1990) The ants. Springer Verlag, Berlin, 732 pp.
- Howlett BE and Davidson DW, 2003. Effects of seed availability, site conditions, and herbivory on pioneer recruitment after logging in Sabah, Malaysia. *Forest Ecology and Management* 184: 369-383.
- Inui Y, Itioka T, Murase K, Yamaoka R and Itino T, 2001. Chemical recognition of partner plant species by foundress ant queens in *Macaranga-Crematogaster* myrmecophytism. *Journal of Chemical Ecology* 27: 2029-2040.
- Janzen DH, 1967. Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *Kansas Science Bulletin* 47: 315-558.
- Jürgens A, Feldhaar H, Feldmeyer B and Fiala B, 2006. Chemical composition of leaf volatiles in *Macaranga* species (Euphorbiaceae) and their potential role as olfactory cues in host-localisation of foundress queens of specific ant partners. *Biochemical Systematics and Ecology* 34: 97-113.
- Kaspari M, Pickering J, Longino JT and Windsor D, 2001a. The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. *Behavioral Ecology and Sociobiology* 50: 382-390.
- Kaspari M, Pickering J and Windsor D, 2001b. The reproductive flight phenology of a neotropical ant assemblage. *Ecological Entomology* 26: 245-257.
- Longino J T, 1991. *Azteca* ants in *Cecropia* trees: Taxonomy, colony structure, and behaviour. In: Huxley CR, Cutler DF (eds.) *Ant-Plant Interactions*. Oxford Univ. Press, Oxford, pp 271-288
- Markin GP and Dillier JH, 1971. Seasonal life cycle of imported fire ants, 565- Hymenoptera-Formicidae on the Gulf coast of Mississippi. *Annals of the Entomological Society of America* 64: 562-565.
- Maschwitz U, Fiala B, Moog J and Saw LG, 1991. Two new myrmecophytic associations from the Malay Peninsula: ants of the genus *Cladomyrma* as partners of *Saraca thaipingensis* and *Crypteronia griffithii*. 1. Colony foundation and acquisition of trophobionts. *Insectes Sociaux* 38: 27-35.
- Maschwitz U, Fiala B, Dumpert K, Hashim R and Sudhaus W, 2016. Nematode associates and bacteria in ant-tree symbioses. *Symbiosis* 69: 1-7.
- Moog U, Fiala B, Federle W and Maschwitz U, 2002. Thrips pollination of the dioecious ant plant *Macaranga hullettii* (Euphorbiaceae) in Southeast Asia. *American Journal of Botany* 89(1): 50-59.
- Murase K, Itioka T, Inui Y and Itino T, 2002. Species specificity in settling-plant selection by foundress ant queens in *Macaranga-Crematogaster* myrmecophytism in a Bornean dipterocarp forest. *Journal of Ethology* 20: 19-24.
- Nascimento IC do, Delabie JHC and Della Lucia TMC, 2011. Phenology of mating flight in Ecitoninae (Hymenoptera: Formicidae) in a Brazilian Atlantic Forest location. *Annales Societé Entomologique France (N.S.)* 47: 112-118.
- Nielsen MG, Peng RK, Offenber J and Birkmose D, 2016. Mating strategy of *Oecophylla smaragdina* (Hymenoptera: Formicidae) in northern Australia. *Austral Entomology* 55: 261-267.
- Noordijk J, Morssinkhof R, Boer P, Schaffers AP, Heijerman T and Sykora KV, 2008. How ants find each other; temporal and spatial patterns in nuptial flights. *Insectes Sociaux* 55: 266-273.
- Peeters C and Molet M, 2010. Colonial Reproduction and Life Histories. In: Lach Let al. (eds.) *Ant ecology*. Oxford University Press, Oxford., pp 159-176.
- Pfeiffer M and Linsenmair KE, 1997. Reproductive synchronization in the tropics: the circa-semiannual rhythm in the nuptial flight of the giant ant *Camponotus gigas* Latreille (Hym./Form.). *Ecotropica* 3:21-32
- Rico-Gray V and Oliveira PS, 2007. The ecology and evolution of ant-plant interactions. University Chicago Press, Chicago, 320 pp.
- Staab M and Kleineidam CJ, 2014. Initiation of swarming behavior and synchronization of mating flights in the leaf-cutting ant *Atta vollenweideri* FOREL, 1893 (Hymenoptera: Formicidae). *Myrmecological News* 19: 93-102.
- Torres JA, Snelling RR and Canals M, 2001. Seasonal and nocturnal periodicities in ant nuptial flights in the tropics (Hymenoptera: Formicidae). *Sociobiology* 37: 601-626.
- Tuerke M, Fiala B, Linsenmair KE and Feldhaar H, 2010. Estimation of dispersal distances of the obligately plant-associated ant *Crematogaster decamera*. *Ecological Entomology* 35: 662-671.

- Ueda S, Quek S-P, Itioka T, Inamori K, Sato Y, Murase K and Itino T, 2008. An ancient tripartite symbiosis of plants, ants and scale insects. *Proceedings Royal Society B* 275: 2319-2326.
- Vasconcelos HL, 1993. *Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant.* *Oecologia* 95: 439-443.
- Wuellner CT, 2000. Male aggregation by *Solenopsis richteri* Forel (Hymenoptera : Formicidae) and associated mating behavior in Argentina. *Journal of Insect Behavior* 13: 751-756.
- Yu DW and Davidson DW, 1997. Experimental studies of species-specificity in *Cecropia*-ant relationships. *Ecological Monographs* 67: 273-294.

ASIAN MYRMECOLOGY

A Journal of the International Network for the Study of Asian Ants

Communicating Editor: Adam L Cronin