Resin-foraging by colonies of Trigona sapiens and T. hockingsi (Hymenoptera: Apidae, Meliponini) and consequent seed dispersal of Corymbia torelliana (Myrtaceae)

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Original article

Resin-foraging by colonies of *Trigona sapiens* and *T. hockingsi* (Hymenoptera: Apidae, Meliponini) and consequent seed dispersal of *Corymbia torelliana* (Myrtaceae)*

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Abstract – Resins are a critical resource for stingless bees and resin-collecting bees act as seed dispersers in tropical plants. We describe the diurnal foraging patterns of colonies of *Trigona sapiens* and *T. hockingsi* on resin and pollen. We also document patterns of waste removal and seed dispersal of *Corymbia torelliana*. At most, only 10% of foragers collected resin or dispersed seed. Nevertheless, bees dispersed 1–3 seeds outside the nest per 5 minutes, and 38–114 seeds per day for each nest. The proportion of returning bees carrying pollen was highest in the morning for both species. The proportion of foragers returning with resin loads showed no significant diurnal variation in any season. Waste removal activity peaked in the afternoon for *T. sapiens* and in the morning for *T. hockingsi*. Seed removal peaked in the afternoon in one year only for *T. sapiens*. Bees dispersed thousands of seeds of *C. torelliana* over the season even though only a small proportion of the colony was engaged in seed transport.

stingless bees / mellitochory / seed dispersal / resin / *Corymbia*

1. INTRODUCTION

In stingless bees, individual workers make behavioural decisions that determine the foraging patterns of the colony. Decisions are based on intrinsic factors, and on information from the colony and environment (Biesmeijer and Slaa, 2004). Colonies can show distinct diurnal patterns of foraging, often determined by environmental cues such as temperature, wind speed and solar radiation (Heard and Hendrikz, 1993) and resource availability (Bartareau, 1996; De Bruijn and Sommeijer, 1997; Nagamitsu and Inoue, 2002). Colony foraging patterns in stingless bees have been well studied for pollen and nectar (Biesmeijer et al., 1999a, b; Biesmeijer and Ermers, 1999; Leonhardt et al., 2007) and the behavioural decision process of individual bees is becoming well understood (De Bruijn and Sommeijer, 1997; Biesmeijer et al., 1999a, b; White et al., 2001; Slaa et al., 2003). Plant resins are an essential resource for nest building, and defence, and resin availability limits colony size and growth (Wille and Michener, 1973; Howard, 1985; Roubik, 1989, 2006; Lehmberg et al., 2008). In contrast with pollen and nectar, resin resources are generally unpredictable and short-lived, and are aggressively defended by some species (Armbruster, 1984; Howard, 1985). Colony foraging patterns for resin have not been studied in stingless bees despite the importance of resin resources.

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Resin-foraging bees are critically important for seed dispersal of three plant species: a rainforest eucalypt, *Corymbia torelliana* (Wallace and Trueman, 1995; Wallace et al., 2008); a tree legume, *Zygia racemosa* (Bacelar-Lima et al., 2006); and an epiphyte, *Coussapoa asperifolia* (Garcia et al., 1992; Nunez et al., 2008). Fruits of these species contain resin or waxes, and stingless bees collecting resin or waxes disperse their seeds (Nunez et al., 2008; Wallace et al., 2008). In *C. asperifolia* and *C. torelliana*, stingless bees are the only biotic seed dispersers and fruits show specific adaptations to seed dispersal by bees (Nunez et al., 2008; Wallace et al., 2008). This unusual seed dispersal syndrome, termed mellitochory, has not been recorded in other species.

The mechanisms of mellitochory have been studied in *C. torelliana.* The fruits of *C. torelliana* are hollow, and resin and seeds are presented inside the fruits behind the valve (Wallace and Trueman, 1995). Stingless bees enter the fruit to collect resin and emerge with either resin, or resin and seeds in their corbiculae (Wallace and Trueman, 1995). Around one quarter of resin collectors at fruits carry seeds (Wallace et al., 2008). Bees attempt to dislodge the seed at the fruit and on surrounding leaves (Wallace and Trueman, 1995), but many transport resin and seeds to their nest and discard seeds outside the nest, thus dispersing them (Wallace and Trueman, 1995; Wallace et al., 2008). In *C. torelliana*, *Trigona* spp. disperse seeds greater than 100m from the parent tree and bee dispersal is critical to the tree's population dynamics (Wallace et al., 2008). However, where *C. torelliana* is planted outside its natural range, the interaction with stingless bees is controversial. Stingless bee keepers report that during the fruiting season of *C. torelliana*, bees abandon all other resin sources and neglect normal foraging to collect resin and seeds, and that seeds and resin in some circumstances can cause colony death (Klumpp, 2007). Colony foraging, resin collection and seed dispersal behaviour, especially in the natural range where *C. torelliana* and stingless bees have coevolved, have not been studied.

The aim of this study was to examine colony foraging patterns for resin and the consequent seed dispersal by two species of stingless bees, *Trigona sapiens* and *T. hockingsi* in the natural range of *C. torelliana*. We specifically addressed the following questions: (1) How much colony activity is allocated to resin foraging, seed transport and seed disposal activities? (2) How many seeds are dispersed by stingless bee colonies? (3) what are the diurnal patterns of colony pollen and resin foraging, waste removal and seed dispersal?

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted at Kuranda, Far North Queensland, Australia (E145°38'S16°49'). Two species of *Trigona*, *T. sapiens* and *T. hockingsi* were located in the study area. The site was close to a large natural population of *C. torelliana* and the surrounding vegetation was a mosaic of rainforest and disturbed areas cleared for human occupation. We monitored two nests of *Trigona* over 3 years: *T. hockingsi* at the base of a hollow dead tree and *T. sapiens* in a permanent dwelling. All observations were conducted between December and February, during the fruiting season of *C. torelliana*. Resin foraging patterns of bees change significantly over the fruiting season as resin becomes less available (Wallace et al., 2008). Observation days within each season were carried out within a short period (1 week) on days when the availability of resin was similar. *T. sapiens* and *T. hockingsi* were monitored for 5 days in the 2003 summer. *T. sapiens* was monitored for 4 days in 2004 and 3 days in 2005. Due to collapse of the tree and subsequent death of the colony of *T. hockingsi* in 2004 it was not possible to monitor this species in 2004 and 2005. The *T. sapiens* nest was 100 m to the nearest *C. torelliana* and the *T. hockingsi* nest was 20 m to the nearest *C. torelliana*.

2.2. Bee activity and seed dispersal at the hives

Nest entrances were observed for 15 minutes each hour. At each nest, data were collected on: the number of bees returning and the number of those with pollen in a 5-minute period; the number of bees returning and the number of those with resin or resin and seeds in the corbiculae in a 5 minute period; the

number of bees departing and the number of those with seeds or faeces in a 5-minute period. All observations were repeated on all nests every hour between 08.00h and 17.00h.

2.3. Statistical analysis

For the nest activity data, mean numbers of bees returning and departing and percentages of bees carrying pollen, resin, seed, and waste (i.e. seed or faeces) were calculated for each hour of the day for each nest observed. A log transformation was performed where data were not normally distributed. Data from 2003 were initially analysed with a 3-way ANOVA with species, season and time of day as factors, and for 2004 and 2005, a 2-way ANOVA with season and time of day as factors. Due to significant 2-way and 3-way interactions between species, season and time, each season and species was subsequently analysed separately with one way ANOVAs. Non-parametric data (proportions of bees entering nests with pollen or resin, and proportions of bees leaving nests carrying faeces or seeds) were analysed with a Kruskal-Wallis test for each season. To calculate seed dispersal, the total number of seeds per day was calculated by multiplying the total in each 5 min observation period by 12 and summing for each day. Means and standard errors were calculated over all observation days.

3. RESULTS

3.1. Resin collection and seed dispersal

Resin collection and seed dispersal was only a small fraction of total colony activity in all nests in all seasons (Figs. 1–4, Tab. I). At the peak, only 10% of total foragers returning to the nest were resin collectors (Figs. 2, 4). Foragers carrying seeds into the nest represented between 0.4% and 1.3% of total returning foragers (Tab. I). Departing foragers carrying seed represented between 0.3% and 2.6% of total departing foragers (Tab. I). At the peak of seed dispersal, foragers departing from the nest carried seed on less than 7% of all flights (Figs. 3, 4). Nevertheless, bee activity resulted in 1–3 seeds dispersed outside the nest per 5 minute period during peak times, resulting in dispersal of approximately 38–114 seeds per day for each nest (Tab. I).
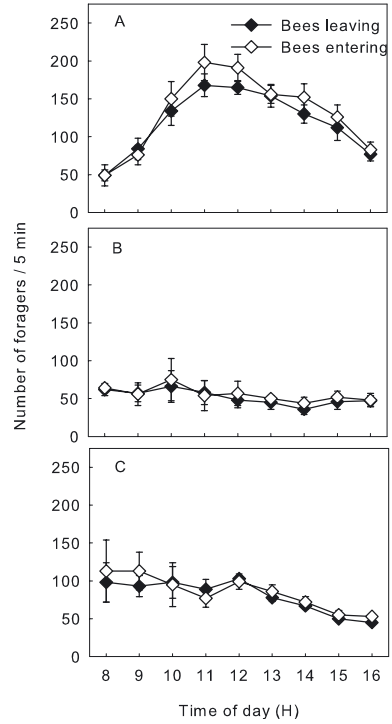

Figure 1. Diurnal patterns in the number of *T. sapiens* leaving and returning to the nest for season 1 (A); season 2 (B); and season 3 (C). The means and standard errors per 5-minute observation are presented. Means are calculated from all days of observation.

3.2. Diurnal patterns of colony foraging

T. sapiens showed diurnal variation in foraging activity in the first season (ANOVA, $P < 0.001$ for both bees departing from the nest and bees returning to the nest) with peaks in bee activity around 12.00 h (Fig. 1A). Diurnal variation in overall activity was not as pronounced in the second season and there were no significant differences between hours of the day in the number of flights (Fig. 1B). There was significant diurnal variation in the third season in the number of bees departing with more activity in the morning (Fig. 1C, ANOVA $P < 0.05$).

The proportion of returning bees of *T. sapiens* carrying pollen in their corbiculae showed significant diurnal variation in the first and

Table I. Daily total number of *Corymbia torelliana* seeds transported, and proportion of foragers (as a % of total activity) engaged in seed transport for each colony and season. Means of all observation days (and standard errors) are presented.

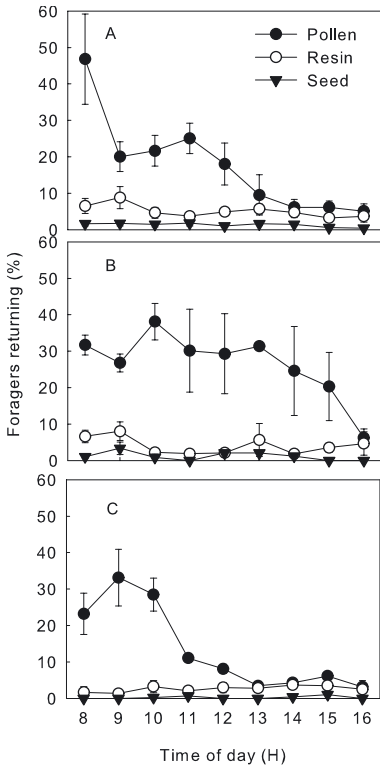|	Total seeds in / day	Foragers returning with seeds (%)	Total seeds out / day	Foragers leaving with seeds (%)
T. sapiens				
Season 1	189.6 (47.9)	1.3 (0.3)	100.8 (28.6)	0.8 (0.3)
Season 2	51.0 (9.0)	1.2 (0.4)	114.0 (36.8)	2.6 (1.0)
Season 3	24.0 (12.0)	0.2 (0.1)	96.0 (12.0)	1.1 (0.1)
T. hockingsi	69.6 (11.0)	0.4 (0.1)	38.4 (12.2)	0.3 (0.1)

Figure 2. Diurnal patterns in the proportion of *T. sapiens* returning to the nest with pollen, resin and seeds for season 1 (A); season 2 (B); and season 3 (C). The means and standard errors per 5-minute observation are presented. Means are calculated from all days of observation.

Figure 3. Diurnal patterns in the proportion of *T. sapiens* leaving the nest with waste and seeds for season 1 (A); season 2 (B); and season 3 (C). The means and standard errors per 5-minute observation are presented. Means are calculated from all days of observation.
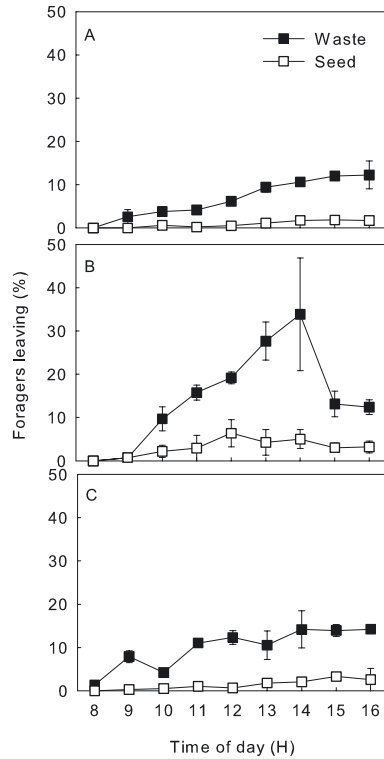
third seasons (Kruskal-Wallis, *P* < 0.001, *P* = 0.002, respectively, Figs. 2A, 2C). Pollen collecting activity was highest in the morning in both seasons. In contrast, the proportion

of foragers returning with resin loads did not show significant diurnal variation in any season (Figs. 2A–C). Waste removal activities peaked in the afternoon, with significant diurnal variation in all seasons (Kruskal-Wallis
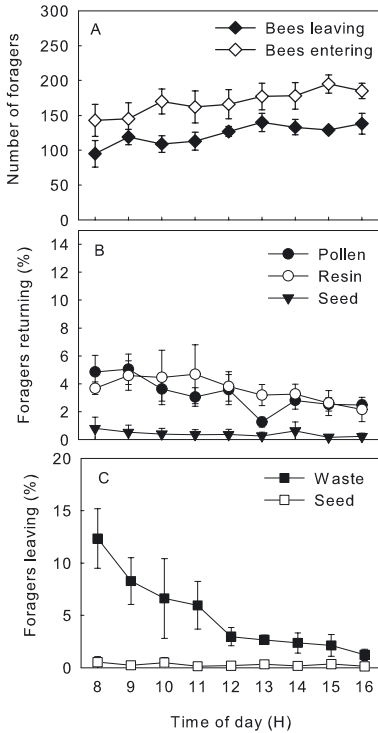
Figure 4. Diurnal patterns in activity of *T. hockingsi*, season 1: (A) number of foragers entering and leaving, (B) proportions of foragers returning with pollen, resin and seeds, (C) proportion of foragers leaving with waste and seeds.

$P < 0.001$, $P = 0.04$, $P = 0.025$, Figs. 3A, 3B, 3C, respectively). In addition, the proportion of bees departing with seed (Kruskal-Wallis, $P = 0.024$) showed significant diurnal variation with peaks in the afternoon in the first season. There were no significant differences in other seasons.

The number of bees engaged in pollen collection and waste removal activities in *T. hockingsi* showed significant diurnal variation (ANOVA, $P = 0.046$, Kruskal-Wallis, $P = 0.013$, respectively) with peaks in the morning in both cases. The number of bees returning, the number of bees leaving, the proportion of resin collection, and seed transport into and out of the colony did not show significant diurnal variations.

4. DISCUSSION

4.1. Resin foraging and seed dispersal

Plant resin is a critical resource for stingless bees (Wille, 1983; Roubik, 1989, 2006) but most resin resources are likely to be unpredictable and short lived (Armbruster, 1984). *C. torelliana* provides a reliable and consistent resin resource over 2–3 months for stingless bees in exchange for seed transport (Wallace et al., 2008). *C. torelliana* has unique fruit adaptations to promote seed dispersal by bees. When fruits dehisce, fruit valves withdraw into the fruit, resulting in a hollow fruit that allows foragers of *Trigona* to enter to collect resin (Wallace and Trueman, 1995). Resin droplets are presented at the margins of the valves in all fruits and, most fruits contain seeds embedded in resin droplets (Wallace et al., 2008). However, seed transport is a significant energetic cost to individual workers, because seeds of *C. torelliana* weigh 2.5–3 mg, approximately 50–60% of the weight of workers (Wallace and Trueman, 1995). Our results show that only a small proportion of foragers in the colony were engaged in seed transport and dispersal activities. At most, only 8% of returning foragers carried a resin load. In other species of stingless bees, resin foragers can account for up to 50% of colony returnees (Leonhardt et al., 2007). Furthermore, only one quarter of returning resin foragers carried a seed, representing only 0.4–1.3% of total returning foragers. Waste removals were a high percentage of outgoing colony flights, but again waste removal bees carrying seeds accounted for less than 2.6% of all outgoing flights. Overall, seed dispersal by the colony accounted for a very small proportion of colony flights, and was a small energetic cost to the colony as a whole. In contrast, pollen foraging peaked at around 50% of returning bees, and many more bees were engaged in pollen foraging than resin foraging. We found no evidence to support claims that bees abandon normal foraging to collect *C. torelliana* resin and seeds, or that *C. torelliana* causes death of colonies (Klumpp, 2007). However, further studies on resin ecology are needed, especially for managed hives in areas where resin resources may be very limited.

Most seeds of *C. torelliana* are dispersed by gravity at fruit opening with only 12% of seeds remaining in the fruit for bee dispersal (Wallace et al., 2008). Eucalypt seeds dispersed by gravity rarely travel more than 50 m and eucalypt seeds of similar size to *C. torelliana* only travel around 20 m when dispersed by gravity and wind (Cremer, 1977). Our results showed that thousands of seeds of *C. torelliana* can be dispersed long distances by a single colony of stingless bees. The colony of *T. sapiens* in this study was 100 m from the nearest *C. torelliana*. We estimated that between 38 and 114 seeds per day were deposited outside of the colony resulting in thousands of seeds dispersed over the 2–3 month fruiting season. Long distance seed dispersal play a crucial role in plant invasions, and rare long distance dispersal events can have a disproportionate influence on plant populations (Richardson et al., 2000; Higgins et al., 2003; Nathan, 2005, 2006). Models of seed dispersal show that even a small proportion of seeds (0.1%) moving long distances can lead to an order of magnitude increase in predicted spread rate (Higgins and Richardson, 1999). Our results confirm that bees may contribute substantially to the spread of *C. torelliana*. The species is rapidly colonising natural forest and is now considered an invasive species in areas where it has been introduced and co-occurs with *T. carbonaria* (Wallace and Trueman, 1995; Wallace et al., 2008).

4.2. Diurnal patterns of colony foraging

Both *T. sapiens* and *T. hockingsi* showed peaks of pollen collecting activity in the morning. Morning peaks of foraging for pollen have been reported in many other species of stingless bee (De Bruijn and Sommeijer, 1997; Nagamitsu and Inoue, 2002). In contrast with pollen foraging, resin foraging was relatively stable over time and did not show diurnal peaks. In other species, individual bees may specialise on one commodity only (pollen, nectar or resin) during a single day, or they may change from early morning pollen or resin collecting to nectar collecting in the afternoon (Biesmeijer and Toth, 1998). Colony foraging

patterns may show early morning and late afternoon peaks in resin collecting, corresponding with lower flight activity for pollen and nectar foraging, or alternatively resin collection may peak when other resources are collected (De Bruijn and Sommeijer, 1997). Resin collection from *C. torelliana* may be partly regulated by resource availability as bees have been observed foraging at fruits of *C. torelliana* until the resin resource was depleted (Wallace et al., 2008). Differences in foraging activity between the years may have been due to different resource availability.

Surprisingly, we found a peak of waste removal and seed dispersal in the afternoon for *T. sapiens* and in the morning for *T. hockingsi*, and on occasions 30% of departing foragers carried waste in their mandibles. The mechanisms regulating colony waste removal are largely unknown. In other studies, high waste removal activity stimulated inexperienced foragers to start foraging (Biesmeijer et al., 1998). Waste removal activity has important consequences for dispersal of seeds of *C. torelliana*, and further studies on stingless bee colony activity and waste removal will help to explain the mechanisms of the unusual seed dispersal syndrome of mellitochory.

Récolte de résine par les colonies de *Trigona sapiens* et de *T. hockingsi* et dispersion consécutive des graines de *Corymbia torelliana*.

abeilles sans aiguillon / *Trigona* / dispersion des graines / résine / Australie

Zusammenfassung – Harzsammelnde stachellose Bienen der Arten *Trigona sapiens* und *T. hockingsi* (Hymenoptera: Apidae, Meliponini) tragen zur Samenverbreitung von *Corymbia torelliana* (Myrtaceae) bei. Harze sind ein wichtiger

Bestandteil der Neststrukturen stachelloser Bienen. Durch das Sammeln von Harz und Wachs aus Früchten tragen diese Bienen entscheidend zur Verbreitung der Samen tropischer Pflanzen über weite Distanzen hinweg bei. Wir beschreiben hier das Harzsammelverhalten von Völkern der stachellosen Bienen *Trigona sapiens* und *T. hockingsi* und die darauf beruhende Verbreitung der Samen von *Corymbia torelliana*. Die Untersuchung erstreckte sich über einen Zeitraum von drei Jahren. Das Harzsammeln und die Samenverbreitung stellt nur einen kleinen Teil der Aktivitäten dieser Völker dar und höchstens 10 % der Arbeiterinnen waren an diese Aktivitäten beteiligt. Nichtsdestotrotz verbreiteten diese Bienen während der Zeiten maximaler Aktivität 1–3 Samen innerhalb von 5 Minuten, bzw. 38–114 Samen pro Tag und Volk. Der Anteil mit Pollenladungen zurückkehrender Bienen zeigte starke tageszeitliche Schwankungen innerhalb der Jahre, wobei die höchste Pollensammelaktivität jeweils morgens zu verzeichnen war. Bei Sammlerinnen, die mit Harzladungen zurückkehrten, waren solche Schwankungen jedoch nicht zu beobachten. Das Heraustragen von Müll zeigte ebenfalls charakteristische Schwankungen im Testverlauf, mit einem Maximum am Morgen bei *T. hockingsi* und einem Maximum am Abend bei *T. sapiens*. Auch das Entfernen von Samen zeigte signifikante Schwankungen im Tagesverlauf, wobei die Maxima bei *T. sapiens* innerhalb eines Jahres in den Nachmittagsstunden lagen. Unsere Ergebnisse zeigen, dass selbst wenn nur ein geringer Anteil der gesamten Sammlerinnen eines Volkes am Samentransport und der Samenverbreitung beteiligt ist, dies dazu führen kann, dass tausende von Samen der Art *C. torelliana* während der 2–3 Monate dauernden Fruchtperiode verbreitet werden können.

Stachellose Bienen / Mellitochorie / Samenverbreitung / Harz / *Corymbia*

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