Flight range of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae)

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Abstract   Bees are key pollinators in both natural and agricultural environments throughout the world. Estimates of the typical distance from their nest that bees will fly to forage are useful when planning their deployment in commercial pollination or ecosystem management. Stingless bees (Meliponini) are social bees that live in colonies comprising a queen and many workers. They pollinate several key tropical crops and can be housed and transported in hives. Thus, there is increasing interest in their use as managed pollinators in regions where they occur naturally, including Australia. Here, we use a mark and release method to estimate the homing range of the most commonly propagated species of Australian stingless bee, *Tetragonula carbonaria* (Smith), where homing range serves as a proxy for foraging flight range. We find the typical and maximum homing range of *T. carbonaria* to be 333 and 712 m, respectively. This range is less than that of the most commonly used commercial pollinator, the honey bee *Apis mellifera* Linnaeus, which we argue confers both advantages and disadvantages on *T. carbonaria* as an alternative crop pollinator.

Key words   crop pollination, foraging range, homing range, Meliponini.

INTRODUCTION

Bees (Apidae) are important as primary pollinators throughout most of the world, both in wild and agricultural environments (Levin 1983; Bawa 1990; Corbet *et al.* 1991). As such, the distance that bees travel to forage directly impacts the successful sexual reproduction of local flowering plants and can shape the spatial and genetic structure of plant communities (Waser *et al.* 1996; Gómez *et al.* 2007). Foraging distances may likewise determine the population structure or density of bees themselves, via competition for resources, or for nest-sites within optimal distance of forage (Zurbuchen *et al.* 2010a). Thus, knowledge of this simple metric for key bee species is of great value to a range of land management practices, including plant conservation and crop pollination.

The most widely used bee for managed crop pollination is the Western honey bee *Apis mellifera*. Today, however, both managed and wild populations of honey bees in many regions of the world are experiencing population instability due to pathogens and pests such as the *Varroa* mite and its associated viruses, and other stressors (Potts *et al.* 2010; Martin *et al.* 2012). Even where honey bees populations are currently stable, the further spread of *Varroa*, and invasive competitors such as *Apis cerana*, poses risks for future population health (Koetz 2013; Iwasaki *et al.* 2015). Native bees offer pollinator diversity and thus insurance against honey bee declines and may even be superior pollinators of some crops (Winfree *et al.* 2007; Garibaldi *et al.* 2013). The stingless bees (Meliponi), a tribe of social bee native to tropical Australia, South and Central America, Asia and Africa,

offer particular promise because their colonies can be propagated and transported in hives. In Australia, interest has mainly focused on one species *Tetragonula carbonaria* (Halcroft *et al.* 2013), which can pollinate the economically important crop macadamia (Heard 1994), and has been proposed as a candidate pollinator for several other crops, including avocado, lychee, blueberry and mango (Halcroft *et al.* 2013). Although their function in wild ecosystems remains poorly researched, stingless bees are likely to also be important plant pollinators and seed dispersers of native vegetation (e.g. Wallace & Trueman 1995).

Tetragonula carbonaria is a small bee, measuring just 4 mm in body length. Body size affects foraging distance nonlinearly, with larger bee species having disproportionately large foraging distances (Greenleaf *et al.* 2007). Even within a colony of the same species, larger individuals may forage at further distances than smaller individuals (Kuhn-Neto *et al.* 2009). Greenleaf *et al.* (2007) collated field estimates of foraging ranges of various bee species to generate a formula in which foraging distance is expressed as a function of a bee's intertegular span. By this formula, the typical foraging range of *T. carbonaria* is estimated between 175 and 562 m. However, to achieve a refined estimate of foraging range, there remains no substitute for field observation and experimentation.

In the field, one can estimate foraging distance using several techniques. First, bees can be trained to an artificial feeder (e.g. Zurbuchen *et al.* 2010b) that is then moved progressively further away from the colony, forcing foragers to decide at what distance the costs of reaching the food source are no longer worthwhile. This technique may prove difficult if natural foraging sources are abundant because bees will be reluctant to train to an artificial feeder or readily abandon it. Second,

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for honey bee species (*Apis* sp.), the 'waggle dance' that is performed by foragers inside the nest to communicate food source locations to nestmates can be decoded to give typical foraging ranges (e.g. Beekman & Ratnieks 2000). Third, for large species, individual foragers can be radar tracked, providing exact foraging paths (e.g. Osborne *et al.* 1999). Finally, bees can be caught and released at increasing distances from the colony, with the percentage of bees that return from each distance providing an estimate of homing range (e.g. Gathmann & Tscharntke 2002). Homing ranges are proxies of foraging ranges under most conditions (Greenleaf *et al.* 2007) and offer the best available approach for estimating foraging distances of small species, which lack complex dance language, and live in a high resource environment, such as *T. carbonaria*.

Here, we estimate the homing range of *T. carbonaria* in a homogeneous agricultural environment, as a proxy of the typical and maximum foraging distances of this important pollinator.

METHODS

We determined the homing range of *T. carbonaria* using five colonies located in a patch of native bushland (approx. 30 m × 120 m), surrounded on all sides by flowering macadamia crops in the Glasshouse Mountains, Queensland, Australia (26° 53′13″S, 152°56′15″E). Hives were positioned at the edge of the bushland such that they faced towards a 700 m stretch of orchard. Colonies were housed in Original Australian Trigona Hive boxes (Heard 2016). We tested each colony once during 1 or 2 days between 3rd and 16th of October 2014. We conducted trials between 9 am and 3 pm on clear sunny days. Daily maximum temperatures during experimental days ranged from 26.1 to 32.9 °C, within the normal foraging temperature range for the species (Heard & Hendrikz 1993). During each trial, we captured seven groups of 20 bees from a colony by placing specimen tubes over the entrance hole and collecting departing foragers. To immobilise the bees, we placed the collected groups in a box of ice for approximately 5 min after which we marked each group with a different colour on the thorax using paint pens (Pentel). Once marked, we stored each group in a specimen container to allow the bees to warm up again before being released.

We released groups of marked bees at 100 m intervals west (270 °) of the colony location beginning at 700 m and ending at 100 m. Although we released all groups of bees in the same direction, this should not influence results, as disorientated bees do not exhibit a directional preference when attempting to return to the colony (Reynolds *et al.* 2007). To release the bees, we opened the specimen container and placed it on a flat white wooden board at ground level until all bees had dispersed. We recorded the time of release for each group.

To enable us to monitor the arrival of the bees at the hive, we partially obstructed the hive entrance by adding a 3 cm long piece of clear plastic 8 mm tubing so that it protruded from the entrance. Newly returning bees were confused by the tubing

and landed on the colony box instead of flying directly in, allowing us to capture marked bees on their return using an aspirator and thereby prevent recounting. We recorded the time and colour of each marked bee that returned up until 3 h after release. To ensure that 3 h was a sufficient trial time to capture most returning bees, we graphed the mean return times for bees released at each distance and used a linear regression to predict the distance from which bees would take more than 3 h to return.

We defined typical and maximum homing ranges as the distances at which 50% and 90% of released bees fail to return (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007). We used a binary logistic regression to determine the effect that release distance had on the chance that bees returned to the colony, including maximum daily temperature on the experimental day and colony ID as covariates (SPSS v. 20). Additionally, we tested for significant differences in the average number of bees returning from each distance using an ANOVA, followed by an S-N-K test to determine which distances were significantly different.

RESULTS

The number of bees that returned to each colony decreased as time progressed and approached zero after approximately 3 h (Fig. 1), indicating that our trial duration was sufficient to capture the majority of returning bees. Additionally, the return times for bees released at each distance (mean ± SD) were well under our 3 h trial duration (Fig. 2).

The number of returning bees significantly declined as release distance increased (Fig. 3; $F_{6,28} = 47.812$, $P < 0.001$). Using S-N-K tests, we could separate return rates into three different subsets ($P < 0.05$) based on release distance, 100–400, 500 and 600–700 m. The number of returning bees significantly dropped between 400 and 500 m, and again between 500 and 600 m (Fig. 3). Using the logistic regression equation, the typical homing range is 333 m, whilst the maximum homing range is 712 m (Fig. 3). Neither temperature nor colony ID was significant predictors of bee returns.
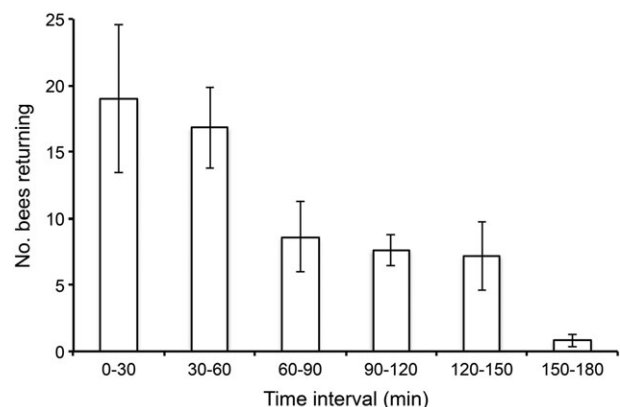

Fig. 1.   Mean number of bees that returned to the colony during each 30 min time period of the experiment, across all five *Tetragonula carbonaria* colonies (error bars indicate ± one standard deviation).
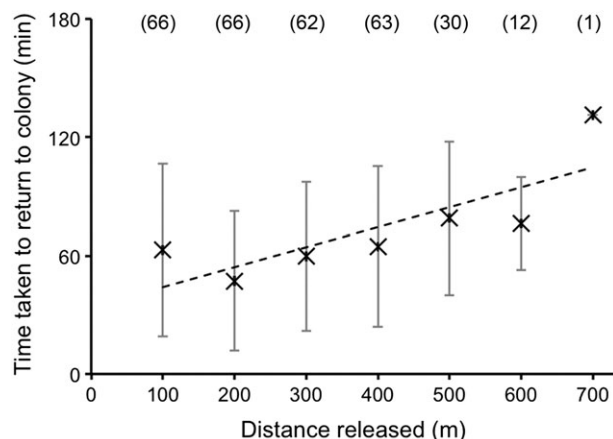
Fig. 2. Mean time taken by those *Tetragonula carbonaria* workers that successfully returned to the colony from each release distance (error bars indicate ± one standard deviation; bracketed numbers indicate number of workers). Assuming a linear relationship between return time and distance released, our experimental period of 180 min was adequate to detect the proportion of bees returning from each distance (dotted line: $y = 0.1x + 33.9$, $R^2 = 0.64$).
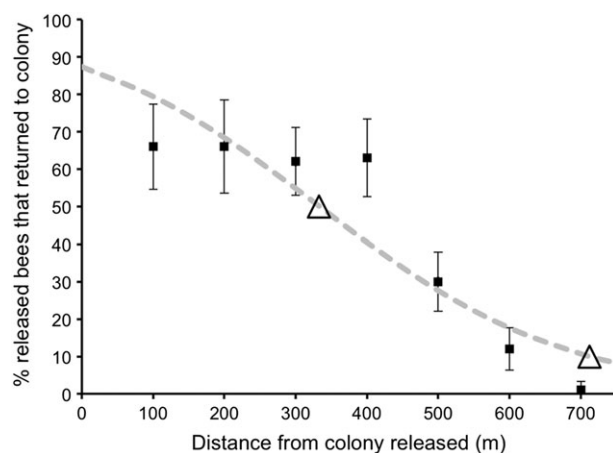

Fig. 3. Mean percentage of bees ($n = 100$ bees per distance) that returned to the colony when released between 100 and 700 m from the colony (error bars indicate ± one standard deviation). The dotted line indicates the logistic regression equation ($y = 1/(1 + e^{-(1.93 - 0.57x)})$, $R^2 = 0.31$) from which was estimated typical and maximum foraging ranges (respectively, the distance at which 50% and 90% of bees return, indicated by triangles).

DISCUSSION

Here, we present the first experimentally based estimate of foraging range for an Australian species of stingless bee. Using homing range as a proxy, we find the typical and maximum foraging distances of *T. carbonaria* to be 333 and 712 m, respectively. Return rates of bees were approximately steady for displacements of any distance up to 400 m from the nest but thereafter declined sharply, suggesting that bees' navigational systems operated best within this radius. This may reflect a reliance on prominent landmarks (Collett *et al.* 2013), where those landmarks were no longer visible at

distances over 400 m, or the use of cognitive spatial maps that cover only the regular foraging area (Menzel *et al.* 2004).

Our estimate of typical foraging distance (333 m) falls within the range predicted by *T. carbonaria*'s small body size (175–562 m, see Greenleaf *et al.* 2007). Estimates based on body size alone cannot account for the, often complex, communication strategies of social bees. Communication between workers inside and outside the nest can result in foragers taking direct routes to forage locations, thus expending less energy in travel and allowing them to travel further. For example, the dance communication of *Apis* sp., whereby workers signal the distance of direction of known food sources (von Frisch 1967), likely accounts for their ability to forage at larger distances than would be expected from their body size (Ratnieks & Shackleton 2015). To date, however, stingless bee foraging ranges have not exceeded size-based predictions (Kerr 1959; Wille 1976; Roubik & Aluja 1983; Greenleaf *et al.* 2007; and this study), suggesting that their communication strategies are comparatively simple (Nieh 2004).

What do our estimates of *T. carbonaria* foraging distance mean for their use as crop pollinators? *T. carbonaria* forage at considerably smaller distances than the dominant pollinator, *A. mellifera*, for which typical foraging distances are near 5 km and maximums greater than 9 km (Beekman & Ratnieks 2000). The smaller foraging range of *T. carbonaria* likely confers both disadvantages and advantages in the context of pollination services. Compared to honey bees, stingless bees nesting in remnant bushland near orchards will not forage far from the remnant, hence may not contribute as much to pollination. Mosaics of bushland and cropland could address this issue. On the plus side, in large orchards, centrally placed hives are likely to be more than 400 m from the orchard edge, and a bees' foraging effort is largely restricted to the crop. In contrast, the large foraging ranges of *A. mellifera* make it difficult to confine them to the target crop, with foragers potentially lost to attractive food sources in surrounding vegetation. The smaller foraging distance may also make *T. carbonaria* better suited to greenhouse pollination. Some stingless bee species of the South American genus *Melipona* have been demonstrated to be efficient pollinators of greenhouse crops (Cruz *et al.* 2005; Del Sarto *et al.* 2005), although whether they achieve better pollination than honey bees in this context remains unclear (Kakutani *et al.* 1993). Two species of Australian stingless bee, including *T. carbonaria*, were found to be efficient pollinators of greenhouse capsicums (Greco *et al.* 2011). Further trials are needed in other key greenhouse crops.

We performed our experiments in a homogeneous agricultural environment, and caution should be used when extrapolating results to native bushland. This is because the mechanisms by which *T. carbonaria* foragers navigate, search and recruit nestmates remain poorly understood. For example, if navigation relies heavily on the use of landmarks, then natural environments, which are more heterogeneous, may allow bees to navigate more easily and potentially extend their foraging ranges (Cartwright & Collett 1983; Plowright & Galen 1985). Nevertheless, our estimates can serve as a useful guide for future efforts to understand the role of stingless bees in pollinating

Australian native flora, and the factors affecting their density and dispersal.

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