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Original article

Foraging behaviour of a blue banded bee, *Amegilla chlorocyanea* in greenhouses: implications for use as tomato pollinators*

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Abstract – Blue-banded bees (*Amegilla* spp.) are Australian native buzz pollinators that are a promising alternative to the introduction of the bumblebee (*Bombus terrestris*) for use as pollinators of tomatoes in Australian greenhouses. The foraging behaviour of *Amegilla* chlorocyanea under greenhouse conditions was monitored in detail. Our results showed that female *Amegilla* are active foragers that make on average 9 pollen foraging flights per day. Using data about flower visitation, we estimated the number of actively nesting female bees needed for adequate pollination in a commercial greenhouse as 282 per hectare.

***Amegilla* / tomato / pollination / greenhouse / foraging / Anthophoridae**

1. INTRODUCTION

Tomatoes grown in greenhouses need special attention to ensure successful pollen transfer to the stigma, as fruit set is generally poor under conditions when natural pollination agents such as wind and insects are withdrawn (e.g. Verkerk, 1957). In numerous countries, several bumblebees species are used for tomato pollination in greenhouses (Velthuis and Doorn, 2004). These large bees buzz the flowers through vibration of the thoracic muscles, which causes a large number of pollen grains to be released onto the stigma. This results in an increase of fruit weight through increased seed set compared to manual pollination using a hand-held vibrating pollination wand (Banda and Paxton, 1991). Bumblebees do not occur on the Australian mainland, and greenhouse tomatoes are generally pollinated using a pollination wand, which has high associated labour costs of approximately A$16 500/ha/y (Carruthers, 2004). The Australian government is presently assessing an application for the importation of live bumblebees. Pressure from the greenhouse tomato industry for the introduction of bumblebees is opposed by conservationists who fear that this poses a significant risk to Australian flora and fauna (Hingston, 2005; Hingston and McQuillan, 1998). Recent studies in New Zealand and Tasmania have shown that bumblebees are efficient pollinators of some introduced weed species (Hergstrom et al., 2002; Stout et al., 2002; Hanley and Goulson, 2003; Goulson and Hanley, 2004).

Studies into alternative Australian native bee pollinators have been undertaken using carpenter bees (*Xylocopa* spp.), which are adequate pollinators of tomato (Hogendoorn et al., 2000). However, carpenter bees are relatively rare in Australia and nearly extinct in the southern parts of the country (Leys, 2000). Therefore, large scale harvesting to establish a breeding population is not an option. The most promising candidates for use as greenhouse tomato pollinators belong to the widely distributed subgenera *Zonamegilla* (Popov, 1950) and *Notomegilla* (Brooks, 1988) in the genus *Amegilla* (Hymenoptera, Apoidea,

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Anthophoridae), commonly known as "blue banded bees" (Dollin et al., 2000).

Hogendoorn et al. (2006) have shown that *A. chlorocyanea* Cockerell is equally effective as bumblebees at buzz pollinating tomato plants in a greenhouse environment, and these bees can be successfully reared and reproduced in artificial nesting substrates in the greenhouse (Bell, unpubl. data; Hogendoorn, unpubl. data).

For the Australian tomato industry to adopt this species as a commercial pollinator, an evaluation is required to determine both the number of bees needed per hectare of greenhouse tomatoes and the costs involved in breeding the bees in sufficient numbers. In this study we present data of foraging behaviour, time allocation, and flower visitation rates of *A. chlorocyanea* in the greenhouse environment in order to estimate the number of bees needed per hectare to achieve adequate pollination.

2. MATERIALS AND METHODS

Foraging and nesting behaviour were observed at three sites. The first site was a small 37 m^2 greenhouse situated at the Waite Campus, The University of Adelaide, South Australia. The greenhouse contained 60 flowering tomato plants (*Lycopersicum esculentum* cv. Conchita) in pots. Throughout the observational period, from November 2004 until April 2005, 10−20 pollen foraging females of *A. chlorocyanea* were present in the greenhouse. The second site was a 1000 m^2 greenhouse located at Virginia, South Australia, containing 1 728 tomato plants (cv. Conchita). The third site was a 750 m^2 hydroponic greenhouse in Loxton SA that contained 6 tomato cultivars. At all sites, the bees used artificial nesting substrate in the form of mud-brick blocks (Hogendoorn et al., 2006), and were fed on a 1:1 solution of honeywater through artificial feeders.

2.1. Foraging activity in the experimental greenhouse

Time-lapse video recording was used to monitor foraging activity in the Waite Campus greenhouse. A total of eight actively nesting females were monitored, 24 hours per day using intervals of 0.18 seconds. Three actively nesting females were observed for 10 days (19 November to 9 December 2004) and five different females were followed during 4 days (16 December 2004 to 10 January 2005). Three indicators of foraging behaviour were recorded: the time of day when females left and re-entered the nest; the presence or absence of pollen on the scopae of the females upon re-entry of their nest; digging activity. Digging episodes started at the first occasion that dirt was removed through the nest entrance and ended after the last dirt had been pushed out. The data were used to calculate timing, duration, and number of pollen and non-pollen ("nectar") flights, time spent inside the nest and time spent digging brood cells. Time allocation was calculated as a percentage of the "total foraging hours", which is defined as the time between start of the first foraging flight in the morning and the end of the last flight in the afternoon. The continuous video observations only allowed a small number of females at a time to be observed. To increase the sample size, information about foraging flight duration was collected during direct observations. *The Observer* software (Noldus, 1991) was used for scoring and analysis of these data. The observations were made during 2 h periods and within 3 time periods from 900h–1100h, 1100h–1500h, 1500h–1800h. Between 17 October 2004 and 30 January 2005, a total of 20 individual females were observed making 344 foraging flights during 83 observational sessions. The mean flight duration of every individual female and the mean number of flights over all the females were calculated.

2.2. Foraging activity in the commercial greenhouse

To investigate the duration and number of pollen flights in the commercial greenhouse, 2 h observations were conducted at Virginia using *The Observer*, during eight visits to the site in February and March 2004. A total of 13 females and 28 completed pollen flights were observed. In addition, 14 one-hour observations were made in Loxton where a total of 40 females and 75 pollen flights were observed between October 2005 and May 2006. The mean flight duration for every individual female and the mean duration of flights over all females were calculated. Using the combined dataset the average number of flights per day was estimated for commercial greenhouses. Furthermore, six actively nesting females were monitored at the Loxton

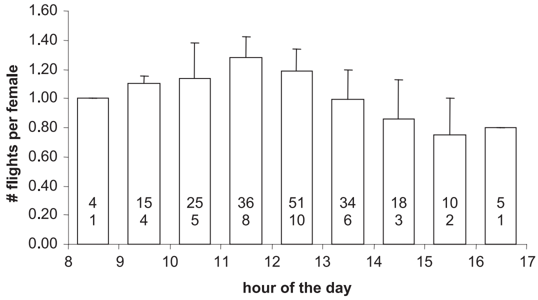

Figure 1. Average number of pollen collecting flights per female per hour in commercial greenhouses. Inside the bars, the number of females and number of hours of observation are given. The average estimated number of pollen flights per day is 9.1 per female.

greenhouse for 2 consecutive days (18 and 19 May 2006). These data allowed confirmation of the number of flights made by each female in a commercial greenhouse.

2.3. Time allocation and number of flowers visited during pollen flights

To investigate the time allocation during pollen collection flights, individual pollen foraging females were followed through the Waite Campus greenhouse. Durations of the following activities were recorded using *The Observer*: sitting, nectar feeding, and foraging on tomato flowers. If a female returned to her nest or if sight of the female was lost during the flight, a new pollen foraging female was selected. To ensure that pollen depletion would not be a factor influencing bee behaviour, the number of tomato flowers visited per unit of time was based on pollen foraging behaviour recorded within one hour after a fresh batch of 80 flowering tomato plants (cv. Conchita) was placed in the greenhouse. Activities of females during a total of 71 pollen-collecting flights were recorded over 16 days. The data were collected between December 2004 and February 2005 and on 17 and 20 May 2006 between 900h and 1700h.

2.4. Statistical analysis

Statistical analyses were performed using SPSS version 11.0 (SPSS Inc., Chicago, Illinois, USA), JMP version 4.0 (SAS Institute Inc., Cary North Carolina, USA), and the data analysis features of Excel 2000 (Microsoft Corp., Seattle, Washington, USA). Means are given with their standard errors.

3. RESULTS

3.1. Daily time allocation

Pollen foraging occurred between 7am and 5pm provided temperatures were above 20 °C, with a slight emphasis on the late morning hours (Fig. 1). Females at the Waite Campus greenhouse spent on average 44.0 ± 1.2% of the potential foraging hours on pollen foraging trips and 8 ± 0.5% of foraging on nectar collecting trips. The remaining 48.2 ± 2.0% of foraging hours was spent inside the nests, where 2.1 ± 0.2% of the time was spent on digging. On average, females remained inside their nest for 11.0 ± 0.4 minutes (n = 8 females, 205 periods) between nectar flights and 29.8 ± 7.9 (n = 8 females, 182 periods) minutes between pollen flights.

3.2. Time allocation during pollen flights and number of flowers visited

By observing females in the greenhouse while they were collecting pollen on fresh, non-depleted tomato plants, time allocation during pollen foraging flights was established. Within a pollen foraging flight, females spent 26 ± 4% of the time collecting pollen, 45 ± 4% of the time sitting, and 29 ± 4% nectar feeding

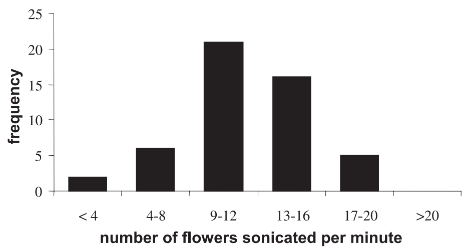

Figure 2. Frequency distribution of the number of tomato flowers buzzed per pollen foraging female per minute.

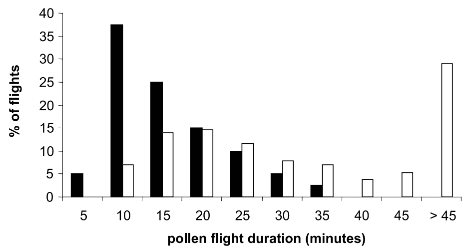

Figure 3. Frequency distribution of the duration of pollen foraging flights in the commercial greenhouse (black bars; n = 53 flights) and in the small experimental greenhouse (white bars, n = 344 flights).

(n = 64). On average, pollen foraging females buzzed 9.3 ± 1.5 (n = 49) flowers per minute. This estimate includes successive visits to the same flower.

3.3. Pollen flight duration

At the Waite Campus greenhouse pollen flights lasted 20–60 minutes, with an average duration of 29.6 ± 1.6 min (28 females, 344 flights; Fig. 2). At the commercial greenhouse in Virginia, pollen flights lasted between 8–33 min, with an average duration of 14.6 ± 1.7 min (14 females, 28 flights), which was not significantly different from the duration of pollen flights in the Loxton greenhouse (12.8 ± 1.5 min, 26 females, 40 flights; $t = 0.45$, d.f. = 38, n.s.). Overall, pollen flight durations in the commercial greenhouses lasted on average 13.4 ± 1.1 min (n = 40 females), which was significantly shorter than in the Waite Campus greenhouse ($t = 8.54$, d.f. = 66; $P < 0.001$).

3.4. Number of pollen flights per day

The eight females that were continually monitored during 14 days in the Waite Campus greenhouse completed 211 foraging trips, yielding an average of 5.6 ± 0.3 trips per day.

For the industrial setting, we investigated the number of flights per day in two ways. Firstly, we combined all one and two hours observations done in Virginia and Loxton, and calculated the number of returns with pollen per actively nesting female per hour (Fig. 1). This estimate reflects averages for all actively nesting females and includes those females were digging during our observations and therefore did not make any pollen flights. The sum of the hourly average number of flights per females gives an estimated number of 9.1 ± 0.54 pollen flights per female per day. Secondly, we monitored the activity of 6 females during two foraging days (18 and 19 May 2006) in the Loxton greenhouse. On average, these females performed 9.17 ± 1.13 flights per day. This average includes data for two females that each spent one day digging new cells, making only nectar flights.

3.5. Bees needed per hectare of tomatoes

The number of bees required per hectare depends on the flowers per hectare, number of foraging trips per female per day and the number of flowers visited per foraging trip. As shown above, the females buzzed on average 9.3 ± 1.5 times per min. Combining these data with the average duration of pollen foraging trips in the industrial greenhouse (13.4 ± 1.1 min), and the number of pollen collecting trips per day (9.1 trips), leads to an estimated average of 1134 buzzes delivered by each actively nesting female per day.

The number of fully mature flowers per Conchita tomato plant in the commercial bee pollinated greenhouse in Loxton was on average 16.0. With 20 000 plants per hectare, there are 320 000 flowers per hectare. Tomato flowers remain open for approximately three days (Morandin et al., 2001a), and therefore 107 000 flowers will need to be pollinated on a daily basis. However, the growth of the fruit benefits from multiple buzzes, and the optimal number of buzzes for the cultivar Conchita by *A. chlorocyanea* is three (Hogendoorn et al., 2006). With 1134 buzzes per female per day, the average number of bees required for a hectare of Conchita tomatoes would be 282 actively nesting females.

4. DISCUSSION

Blue-banded bees are active foragers and perform on average 9 pollen flights per day when foraging in a tomato greenhouse. The accumulated hourly observational data of foraging behaviour in commercial greenhouses and the continuous observation of six actively nesting females yielded very similar results. Both estimates included data for those females that did not collect pollen because they spent a large part of the day digging a new cell.

In the small Waite Campus greenhouse, the average number of flights per day was significantly lower than in the commercial greenhouse, while average flight duration was significantly longer. When encountering diminishing pollen returns, bumblebees have been shown to spend a greater time searching for pollen (Buchmann and Cane, 1989; Shelly et al., 2000), while Shelly et al. (2000) found that *Bombus pullatus* may give up pollen collecting altogether when pollen yield gets low. Thus it is likely that both the smaller number and the longer durations of pollen flights in the Waite Campus greenhouse have been caused by pollen depletion. Because pollen depletion seems to be a major factor influencing the data collected in the Waite greenhouse, we focus on the results for the commercial greenhouse.

How does the estimate of 9.1 pollen flights per day found here compare estimates for other *Amegilla* and other solitary bees? A study of the foraging and nesting behaviour of *A. pulchra* in an urban garden shows that females produce on average 0.7 brood cells per day (our calculations based in Tab. I, Cardale, 1967) and that they make between 10 and 18 pollen flights to produce a brood cell. This implies that 7–12.6 pollen flights are made per day in an urban garden environment, which is similar to our estimate of 9.1 flights per day. Estimates of around ten pollen flights per day have also been found for *Chelostoma florisomne* (Munster-Swendsen and Calabuig, 2000), and *Xylocopa* species (Velthuis et al., 1984). By contrast, bumblebee workers have been estimated to perform 3−6 pollen trips per day for *B. terrestris* when foraging in the field (Spaethe and Weidenmuller, 2002), and 2.4−4.8 flights per day per worker *B. impatiens* in a tomato greenhouse (Morandin et al., 2001b).

The average number of buzzes per pollen collecting flight on fresh flowers at the Waite Campus greenhouse was 9.3 per minute, giving an average of 125 buzzes per pollen flight in the commercial greenhouse. Based on a required three buzzes per flower for optimal pollination of cv. Conchita (Hogendoorn et al., 2006), the number of bees needed per hectare for adequate pollination of this cultivar was estimated as 282.

It is likely that the number of bees needed for pollination changes with the tomato cultivar. Conchita is a cherry tomato with a large number of relatively small flowers whereas various standard or beefsteak cultivars, have less flowers that are larger and produce more pollen and these aspects influence flower visitation frequency in bumblebees (Lefebvre and Pierre, 2006). Therefore it is possible that a different number of bees are needed to pollinate standard and beefsteak cultivars. In addition, it is likely that a reduction of both day length and temperatures during winter will decrease the number of foraging flights per day. In that case, more females could be needed during the winter months.

It is interesting to know how our estimate of 282 female *Amegilla* per hectare compares to the number of bumblebees prescribed for the tomato industry. Industrial recommendations are to use 10−15 commercial bumblebee colonies per hectare, each containing 50−60 workers (Morandin et al., 2001a; Ravenstijn and Sande, 1991). This would equate to approximately 500−900 bumblebee workers per hectare. With an average of 4.8 pollen-collecting flights per worker per day

(Morandin et al., 2001b), this would result in at least 2400 bee trips per hectare (Morandin et al., 2001b). The estimated number of blue-banded bee trips needed per hectare was 2566 (282 bees, 9.1 flights). However, flower visitation rates have not been quantified for *Bombus* inside the greenhouse. For this reason, further comparisons of performance are not feasible at this stage.

Hogendoorn et al. (2006) have shown that blue-banded bees' pollination can cause a 20% increase in tomato weight compared to wand pollination. The present study shows that female *A. chlorocyanea* are active foragers inside commercial greenhouses. These traits make blue-banded bees a suitable native alternative to the introduction of bumblebees for pollination of greenhouse tomatoes. Ongoing research is underway to develop a breeding program that will allow a reliable industrial supply of these bees.

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Comportement de butinage de l'abeille *Amegilla chlorocyanea* sous serre : implications pour son utilisation comme pollinisateur de la tomate.

***Amegilla* / Anthophoridae / pollinisation / tomate / *Lycopersicum esculentum* / comportement de butinage / culture protégée**

Zusammenfassung – Das Sammelverhalten der blaugebänderten Biene *Amegilla chlorocyanea* in Gewächshäusern und dessen Bedeutung für ihre Verwendung als Bestäuber für Tomaten. In Gewächshäusern gezogene Tomaten benötigen Hilfen bei der Bestäubung. In vielen Ländern werden Hummeln als Bestäuber eingesetzt, hierdurch wird ein im Vergleich zur arbeitsaufwändigen manuellen Stabbestäubung höherer Ertrag erzielt. Auf dem australischen Kontinent kommen Hummeln nicht vor und die australische Regierung prüft zur Zeit einen Antrag der tomatenerzeugenden Industrie auf die Einfuhr von Hummeln. Die Naturschützer wenden sich dagegen, da sie ernsthafte Auswirkungen der Einfuhr eines neuen Bestäubers auf die Umwelt befürchten, insbesondere durch die Bestäubung von bestehenden oder „schlafenden“ Unkräutern. Blaugebänderte Bienen (*Amegilla* spp.) sind einheimische australische „buzz“ Bestäuber, die Tomaten bestäuben können und dort eine ähnliche Steigerung der Erträge bewirken wie Hummeln (Hogendoorn et al., 2006). Falls sie in genügenden Anzahlen gezüchtet werden können, könnten sie daher eine wertvolle Alternative für den australischen Tomatenanbau darstellen. In diesem Artikel wird eine detaillierte Studie des Sammelverhaltens von *Amegilla chlorocyanea* in Gewächshäusern vorgestellt mit dem Ziel, die Anzahl der pro Hektar von Gewächshaustomaten benötigten Bienen zu ermitteln. Mittels einer Videobeobachtung der Nistaktivität über 24 Stunden konnten wir zeigen, dass die weiblichen *A. chlorocyanea* aktive Sammlerinnen sind, die in kommerziellen Gewächshäusern pro Tag im Mittel 9 Pollensammelflüge durchführen. Durch Verfolgen der Sammlerinnen während der Sammelaktivitäten konnten wir abschätzen, dass eine Sammlerin etwa 110 Blüten pro Tag „buzz“ bestäubt. Anhand dieser Daten lässt sich abschätzen, dass für eine angemessene Bestäubung eines Hektars Gewächshaustomaten etwa 280 Pollensammlerinnen benötigt werden. Zur Zeit laufen Untersuchungen zur Entwicklung eines Zuchtprogramms, durch das eine verlässliche industrielle Versorgung mit diesen Bienen erreicht werden soll.

***Amegilla* / Tomaten / Bestäubung / Gewächshäuser / Sammeln / Anthophoridae**

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