MS BERNADETTE WITTWER (Orcid ID : 0000-0002-5531-2939)

PROFESSOR MARK ELGAR (Orcid ID : 0000-0003-0861-6064)

Article type : Research Paper

Editor: J. Wright

Cryptic castes, social context and colony defence in a social bee, *Tetragonula carbonaria*

Short title: Cryptic castes and colony defence in a social bee

Bernadette Wittwer¹, Mark A. Elgar¹

¹ School of BioSciences, University of Melbourne

Corresponding author:

Bernadette Wittwer

School of BioSciences

University of Melbourne

Parkville, Victoria, 3010, AUS

Email: berniewittwer@gmail.com

Phone: (61) 415147616

Acknowledgments

Many thanks go to Tim Heard for arranging access to the colonies, advice on experimental design and *T. carbonaria* behaviour.

Conflict of interest

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/eth.12765](https://doi.org/10.1111/eth.12765)

This article is protected by copyright. All rights reserved

We declare we have no conflict of interest

Abstract

Division of labour in social insect colonies is facilitated in two ways: through temporal sharing of tasks or by morphologically specialised castes. In casteless species, colony defence is maintained by morphologically indistinct workers, who lack the obvious defensive specialization of polymorphic species. Discrimination of intruders is carried out via antenna, which also detect defensive social cues such as alarm pheromones. Despite their functional importance however, antennal morphology is rarely considered in studies of nestmate recognition. We investigated antennal morphology and the necessity of social cues in mediating defensive behaviour across differentially tasked workers of a casteless social bee, *Tetragonula carbonaria*. Our results suggest that the current understanding of division of labour in casteless worker species remains poorly understood, with differences in antennal morphology and aggression creating morphologically and behaviourally distinct 'cryptic castes'. Further, we found that defensive behaviour was only elicited near nest odours, highlighting the importance of mediating aggression among workers.

Keywords: caste, nestmate recognition, task allocation, antenna, *Tetragonula carbonaria*

Introduction

Division of labour in social insect societies is essential for colony organization and maintenance. Often, it is facilitated by worker dimorphism and the evolution of highly specialised castes (Wilson 1984; Fjerdingstad & Crozier 2006). In these societies, workers are behaviourally variable and task allocation is static. Guards are among the most specialised castes in highly polymorphic species, possessing distinctive morphological and behavioural characteristics: nestmate recognition studies repeatedly reveal that these workers are more aggressive than their typically smaller nestmates (Whitehouse & Jaffe 1996; Grüter et al. 2012). In contrast, task allocation changes temporally in species with morphologically indistinct workers. Typically, workers in these species spend the first weeks after eclosion engaging in in-nest duties such as nursing, then progress to guard behaviour and eventually foraging (Robinson 1987; Gordon et al. 2005). In these casteless worker societies, a lack of specialization suggests that each individual is similarly capable of engaging with intruders and defending the nest.

Nest defence is of paramount importance to social insects that are frequently attacked by predators, parasites and conspecific intruders (Breed & Page 1991). Nest defence in both

casteless and polymorphic worker species requires two steps: distinguishing between nestmates and others, and an appropriate behavioural response (Leonhardt et al. 2016). Among bees, sensilla on the antennae and legs detect the cuticular profiles (CHC's) of other individuals. Olfactory receptors in the sensilla bind odour molecules, stimulating sensory neurons that are then decoded in specialised regions of the brain (Kaissling 1971; Hildebrand 1995). Bees use CHC's to distinguish between nestmates and other intruders, and an unfamiliar profile typically causes an aggressive response (van Zweden & d'Ettorre 2010).

Antennae have an additional function involved with nest defence – the detection of cues that may motivate workers to react aggressively. Volatile signals, such as alarm pheromones, encourage defensive behaviour (Blum 1969), but more subtle social signals emanating from the nest may similarly activate a response (Couvillon et al. 2013). Given the functional importance of antennae, it is surprising that antennal morphology is rarely, if ever, considered in studies of nestmate recognition (but see (Gill et al. 2013)).

Workers in the eusocial meliponine bee *Tetragonula carbonaria* are morphologically identical and, like other meliponine species (Sakagami 1982; Sommeijer 1984; Inoue et al. 1996; Grüter et al. 2017), task allocation is assumed to be associated with age, although some meliponine species have evolved behaviourally distinct sub-castes (Hammel et al. 2016; Grüter et al. 2017). Guards in *T. carbonaria* are visible at the entrance and challenge returning workers and potential intruders (Gloag et al. 2008). If an intruder is detected, they are removed by a guard in a physical contest that is usually fatal for both combatants, ensuring the cost of misidentification is high (Gloag et al. 2008; Cunningham et al. 2014; Shackleton et al. 2015). We examined variation in antennal morphology and social cues across guards and foragers in this casteless species, and determined their role in nestmate recognition and defence. Specifically, we asked the following questions: (1) does the response of bees to non-nestmates depend upon their proximity to nest odours; (2) do guards and foragers respond differently to non-nestmates; and (3) do guards and foragers differ in antennal morphology?

Methods

Colonies of *T. carbonaria* (n=5) used in our experiments were sourced from distinct and unrelated wild colonies and raised in artificial hive boxes in suburban Brisbane, Australia. Hive boxes contain a nest of around 8kg, similar to that of established wild colonies (Heard 2016). Foragers were caught in the air, using a clean plastic bag. Guards form a distinctive ring at the nest entrance and were captured in a glass vial. Vials were used once only, to

eliminate contamination through volatile or cuticular odours. Our sample includes workers of a range of ages because brood of *T. carbonaria* is produced continuously (Heard 2016).

Trials

A forager or guard (focal bee) was chosen from the holding container and placed in the test arena with a stimulus bee that was either a forager nestmate or forager non-nestmate. Only the behaviour of the focal bee was monitored.

The effect of social context was examined by employing two sets of assays: the first was conducted in an enclosed glass container washed with hexane between trials (Fig. 1a); and the second was conducted in a tube that was attached to the nest entrance (Fig. 1b). The container in the first trial was located roughly 6-8 metres from the nest. In the second trial, gauze was placed between the colony entrance and the test arena, allowing passage of volatile chemical odours, but not bees, into the test arena. In both assays, bees were allowed to acclimatize for one minute before being introduced to each other.

Trials only began once the bees had encountered each other, thereby accounting for any effects of different sized containers. Each trial was then filmed (Sony DSCH90) for three minutes. The digital recordings were replayed, and we noted the frequency of the following behaviours of the focal bee: antennating or mutual touching of the antenna (typically associated with mutual identification). Chasing, (one bee pursues the other, usually accompanied by antennating on the abdomen of the escaping bee), a behaviour common in *Apis mellifera* (Breed et al. 2004) and other meliponines (Inoue et al. 1999); and grasping/fighting with mandibles and legs preventing either bee from escaping. This fighting behaviour is often observed in this species and can involve a swarm of thousands of workers (Heard 1996; Gloag et al. 2008; Cunningham et al. 2014).

Each of the four treatments were replicated with ten trials, using a randomized collection of bees from across the five colonies. Colony identity and treatment were not confounded, and the behavioural data were collected blind to task and nestmate status.

Morphological assays

After each trial, the focal bees were euthanized in a freezer. The antennae were removed from the head and dehydrated through ethanol solutions of 75, 80, 85, 90, 95, and 100%. Antenna were critically dried (Balzers CPD 030), then sputter coated with gold and photographed in a scanning electron microscope (Phillips XL30 FEG). Sensilla density was calculated across the middle two segments (five and six) and the most distal segments (nine

and ten) of the antenna. We manually counted the number of sensilla present within three quadrats drawn onto each segment using ImageJ v1.49 with the Cell Counter package (Schneider et al. 2012). The value across the quadrats was averaged, giving a mean value for density per 1000 μm^2 . Body size, measured by intertegular distance, and head width, measured as the widest point of the head viewed from above, were also calculated in ImageJ.

Statistical analysis

We calculated an aggression index, following (Gill et al. 2013):

$$\frac{\sum_i^3 (A_i \times f_i)}{n}$$

where A_i denotes the assigned aggression score for each behaviour i , f is the frequency of the behaviour and n is the number of all behaviours recorded. The behaviours were assigned the following scores: antennation – 1; chasing – 2; grasping/fighting – 3.

We included antennation behaviour in the index because it represents an important component of nestmate discrimination (see Breed et al., 2004), and also because we observed bees persistently chasing and antennating non-nestmates, suggesting that the behaviour has functions beyond ‘exploratory’ behaviour. Aggression and density scores were compared using mixed models, with colony as a random effect, in JMP (v12.1), and pairwise comparisons for aggression were analysed using Tukey’s post hoc test.

Results

Social context

Bees in the sealed glass container displayed none of the behaviours observed in typical worker-to-worker interactions in natural populations. Instead, the bees spent most of their time attempting to locate a point of escape. In contrast, when the assay container was connected to the nest, bees interacted frequently, and antennation, at a minimum, was recorded during each trial, (see electronic supplementary material). There was a significant difference in their behaviour across the four treatments ($F_{3, 41} = 65.5866$, $p < 0.001$). The mean aggression scores of foragers and guards against test nestmate bees were low (Fig. 2a), and did not strongly differ between tasks (Tukey’s *post hoc* test, $p = 0.0557$). Conversely, both focal guards and foragers reacted aggressively towards non-nestmate test bees, and their scores were markedly different between tasks (Tukey’s *post hoc* test, $p < 0.001$), with the mean aggression scores of guards 1.2 times greater than that of foragers.

The antennation frequency of focal foraging bees toward non-nestmate foragers (**Fig. 2b**) was significantly higher than focal guard; the mean frequency of foragers is 1.9 times higher than that of guards (Tukey's *post hoc* test, $p=0.0161$).

Morphological assays

The sensilla density of both foragers and guards increased distally along the length of the antenna (**Fig. 3**). However, regardless of segment, sensilla density was significantly higher in guards compared with foragers ($F_{(1,38)} = 5.0368$, $p=0.0369$). Guards are also significantly larger than foragers. The intertegular distance of guards (**Fig. 4**) ($1.188\text{mm} \pm 0.0273$) is significantly larger than that of foragers (1.109 ± 0.0197), a mean difference of approximately 7% ($t_{(18)} = 2.1001$, $p = 0.0302$). Comparative results of head width are also consistent with intertegular distance; the heads of guards (**Fig. 5**) ($1.857\text{mm} \pm 0.0146$) are significantly wider than that of foragers (1.787 ± 0.0147), a difference of approximately 4% ($t_{(18)} = 2.1009$, $p = 0.0032$).

Discussion

The response of workers of *T. carbonaria* to conspecifics depends upon both social context and task. When isolated from their nest, workers did not interact with each other, but they displayed inquisitive and aggressive behaviour towards one another in the presence of nest odours. In these encounters, guards were more aggressive than foragers, reflected by a greater willingness to physically engage with intruders. Workers are not only behaviourally distinct but morphologically different; guards are both larger, and have significantly greater numbers of antennal sensilla than foragers.

Our experiments highlight the importance of nest context in eliciting defensive behaviour in *T. carbonaria*. Workers are likely to be able to detect their own nests through chemical odours from the nest material, which in meliponines, is often similar to the workers cuticular profile (Leonhardt et al. 2011a). This may allow guards to readily compare the cuticular profiles of returning workers against nest odour. In addition, workers in close proximity to the nest may also respond to vibrational signals that may reveal nest identity (Hunt & Richard 2013). The importance of workers confining their defensive behaviour to the critical area of the nest entrance may reflect the potential cost of recognition errors: experimentally induced defensive swarm responses from a *T. carbonaria* colony revealed that one in five workers engaged in fatal fighting had inadvertently coupled with a nestmate (Gloag et al. 2008). In addition, these fighting swarms may last for several days, seriously affecting the ability of the colony to forage. Given the cost of these antagonistic encounters, there is a strong

functional benefit to ensuring that defensive behaviour is context-specific. Our results may help explain the surprisingly low levels of aggression towards non-nestmates in other bees, revealed from trials in isolated arenas (Leonhardt et al. 2011b; Dew et al. 2014) but see (Breed & Page 1991). Social context is also important in honey bees, whose defensive behaviour is usually only expressed at the nest entrance and environmental or social cues may be required to discriminate nestmates (Downs & Ratnieks 1999; Buchwald & Breed 2005). Similarly, gynes of *Polistes fasciatus* that are not exposed to their natal nest struggle to discriminate between related and non-related females (Shellman & Gamboa 1982). Future nestmate recognition studies should consider the role of social odours when measuring aggression, or they may fail to capture the full range of behaviours performed in nest defence (Breed 2003).

The consistent pattern of differential investment in antennal sensilla between guards and foragers likely reflects differences in required capacity to detect signals. Guards are the frontline defence of the nests of meliponine bees, and threats of usurpation from neighbouring conspecific colonies are common (Cunningham et al. 2014; Grüter et al. 2016). In bumblebees, larger workers have a higher density of olfactory antennal sensilla and greater odour sensitivity (Spaethe et al. 2007). Similarly, higher sensilla density may allow *T. carbonaria* guards to identify intruders more quickly and or accurately than foragers, especially if these sensilla contain receptors for nest recognition signals. This interpretation of a link between sensilla density and efficient signal detection is consistent with reported differences in the density of sensilla between social and solitary bees, which presumably reflect a greater investment in antennal receptor organs in social species (Wittwer et al. 2017).

Constraining the definition of worker castes to obvious gross polymorphisms may be unhelpful, as differences in finer morphological structures may create 'cryptic castes' within worker populations. We use 'cryptic' to indicate that the morphological differences are simply less obvious than in 'conventional' castes – in a manner analogous to 'cryptic' female choice and 'cryptic' species. Although foragers in our assays chased and antennated more often than guards, only guards attacked non-nestmate intruders. Soldier or guard castes of polymorphic social insects are also typically larger and have elevated levels of aggression (Jandt & Dornhaus 2009; Kamhi et al. 2015). A larger body and greater head width may benefit guards, who are most likely to engage intruders in physical contests, where a large body size is likely to be useful. Our results are consistent with a recent study documenting worker differentiation in ten other stingless bee species (Grüter et al. 2017), where size and colour dimorphism is associated with previously unknown guard castes. Age polyethism

(Wilson 1971) is not precluded as a driver of task allocation in *T. carbonaria*: younger workers may remain in the nest, engaging in in-nest duties, subsequently adopting either foraging or guarding tasks depending upon their sensilla density. Indeed, some guards may subsequently become foragers, perhaps if their antennae are damaged (see Gill et al., 2012). Accordingly, we predict far greater variation in the body and antennal size of younger workers confined to the nest.

Variation in antennal morphology in these previously unnoticed cryptic castes allows *T. carbonaria* to produce workers optimally positioned to defend their colonies. Odour mediated aggression ensures workers maintain behavioural plasticity, thereby giving the colony a flexible and efficient response to threats.

References

- Blum, M. S. (1969). Alarm Pheromones. *Annual Review of Entomology*, 14, 57-80.
- Breed, M. D. (2003). Nestmate recognition assays as a tool for population and ecological studies in eusocial insects: a review. *Journal of the Kansas Entomological Society*, 539-550.
- Breed, M. D., Guzmán-Novoa, E. & Hunt, G. J. (2004). Defensive behavior of honey bees: organization, genetics, and comparisons with other bees. *Annual Reviews in Entomology*, 49, 271-298.
- Breed, M. D. & Page, R. E. (1991). Intra-and interspecific nestmate recognition in *Melipona* workers (Hymenoptera: Apidae). *Journal of Insect Behavior*, 4, 463-469.
- Buchwald, R. & Breed, M. D. (2005). Nestmate recognition cues in a stingless bee, *Trigona fulviventris*. *Animal Behaviour*, 70, 1331-1337.
- Couvillon, M. J., Segers, F. H., Cooper-Bowman, R., Truslove, G., Nascimento, D. L., Nascimento, F. S. & Ratnieks, F. L. (2013). Context affects nestmate recognition errors in honey bees and stingless bees. *Journal of Experimental Biology*, 216, 3055-3061.
- Cunningham, J. P., Hereward, J. P., Heard, T. A., De Barro, P. J. & West, S. A. (2014). Bees at War: Interspecific Battles and Nest Usurpation in Stingless Bees. *Natural History*, 184.

284 Dew, R. M., Gardner, M. G. & Schwarz, M. P. (2014). The problems of a priori
 285 categorisation of agonism and cooperation: Circle - tube interactions in two
 286 allodapine bees. *Ethology*, 120, 551-562.

287 Downs, S. G. & Ratnieks, F. L. (1999). Recognition of conspecifics by honeybee
 288 guards uses nonheritable cues acquired in the adult stage. *Animal Behaviour*,
 289 58, 643-648.

290 Fjerdingstad, E. & Crozier, R. (2006). The evolution of worker caste diversity in
 291 social insects. *The American Naturalist*, 167, 390-400.

292 Gill, K. P., van Wilgenburg, E., Macmillan, D. L. & Elgar, M. A. (2013). Density of
 293 antennal sensilla influences efficacy of communication in a social insect. *The*
 294 *American Naturalist*, 182, 834-840.

295 Gloag, R., Heard, T., Beekman, M. & Oldroyd, B. (2008). Nest defence in a stingless
 296 bee: What causes fighting swarms in *Trigona carbonaria* (Hymenoptera,
 297 Meliponini)? *Insectes Sociaux*, 55, 387-391.

298 Gordon, D., Chu, J., Lillie, A., Tissot, M. & Pinter, N. (2005). Variation in the
 299 transition from inside to outside work in the red harvester ant *Pogonomyrmex*
 300 *barbatus*. *Insectes Sociaux*, 52, 212-217.

301 Grüter, C., Menezes, C., Imperatriz-Fonseca, V. & Ratnieks, F. (2012). A
 302 morphologically specialized soldier caste improves colony defense in a
 303 neotropical eusocial bee. *Proceedings of the National Academy of Sciences*,
 304 109, 1182-1186.

305 Grüter, C., Segers, F., Menezes, C., Vollet-Neto, A., Falcón, T., von Zuben, L.,
 306 Bitondi, M., Nascimento, F. & Almeida, E. (2017). Repeated evolution of
 307 soldier sub-castes suggests parasitism drives social complexity in stingless
 308 bees. *Nature Communications*, 8, 4.

309 Grüter, C., von Zuben, L., Segers, F. & Cunningham, J. (2016). Warfare in stingless
 310 bees. *Insectes Sociaux*, 63, 223-236.

311 Hammel, B., Vollet-Neto, A., Menezes, C., Nascimento, F. S., Engels, W. & Grüter,
 312 C. (2016). Soldiers in a stingless bee: work rate and task repertoire suggest
 313 they are an elite force. *The American Naturalist*, 187, 120-129.

314 Heard, T. (1996). Stingless bees. *Nature Australia*, 1996, 50-55.

315 Heard, T. (2016). The Australian native bee book. West End: Sugarbag Bees.

- 316 Hildebrand, J. G. (1995). Analysis of chemical signals by nervous systems.
317 *Proceedings of the National Academy of Sciences*, 92, 67-74.
- 318 Hunt, J. & Richard, F.-J. (2013). Intracolony vibroacoustic communication in social
319 insects. *Insectes Sociaux*, 60, 403-417.
- 320 Inoue, T., Roubik, D. & Suka, T. (1999). Nestmate recognition in the stingless bee
321 *Melipona panamica* (Apidae, Meliponini). *Insectes Sociaux*, 46, 208-218.
- 322 Inoue, T., Salmah, S. & Sakagami, S. F. (1996). Individual variations in worker
323 polyethism of the Sumatran stingless bee, *Trigona (Tetragonula)*
324 *minangkabau* (Apidae, Meliponinae). *昆蟲*, 64, 641-668.
- 325 Jandt, J. M. & Dornhaus, A. (2009). Spatial organization and division of labour in the
326 bumblebee *Bombus impatiens*. *Animal Behaviour*, 77, 641-651.
- 327 Kaissling, K.-E. 1971: Insect olfaction. In: Olfaction. Springer. pp. 351-431.
- 328 Kamhi, J. F., Nunn, K., Robson, S. K. & Traniello, J. F. (2015). Polymorphism and
329 division of labour in a socially complex ant: neuromodulation of aggression in
330 the Australian weaver ant, *Oecophylla smaragdina*. *Proceedings of the Royal*
331 *Society Biological Sciences Series B*, 282, 20150704.
- 332 Leonhardt, S. D., Blüthgen, N. & Schmitt, T. (2011a). Chemical profiles of body
333 surfaces and nests from six Bornean stingless bee species. *Journal of*
334 *Chemical Ecology*, 37, 98-104.
- 335 Leonhardt, S. D., Form, S., Blüthgen, N., Schmitt, T. & Feldhaar, H. (2011b). Genetic
336 relatedness and chemical profiles in an unusually peaceful eusocial Bee.
337 *Journal of Chemical Ecology*, 37, 1117-1126.
- 338 Leonhardt, S. D., Menzel, F., Nehring, V. & Schmitt, T. (2016). Ecology and evolution
339 of communication in social insects. *Cell*, 164, 1277-1287.
- 340 Robinson, G. E. (1987). Regulation of honey bee age polyethism by juvenile
341 hormone. *Behavioral Ecology and Sociobiology*, 20, 329-338.
- 342 Sakagami, S. F. (1982). Stingless bees. *Social insects*, 361-423.
- 343 Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25
344 years of image analysis. *Nature Methods*, 9, 671-675.
- 345 Shackleton, K., Al Toufailia, H., Balfour, N. J., Nascimento, F. S., Alves, D. A. &
346 Ratnieks, F. L. (2015). Appetite for self-destruction: suicidal biting as a nest
347 defense strategy in *Trigona* stingless bees. *Behavioral Ecology and*
348 *Sociobiology*, 69, 273-281.

- Shellman, J. S. & Gamboa, G. J. (1982). Nestmate discrimination in social wasps: the role of exposure to nest and nestmates (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behavioral Ecology and Sociobiology*, 11, 51-53.
- Sommeijer, M. J. (1984). Distribution of labour among workers of *Melipona favosa* F.: Age-polyethism and worker oviposition. [journal article]. *Insectes Sociaux*, 31, 171-184.
- Spaethe, J., Brockmann, A., Halbig, C. & Tautz, J. (2007). Size determines antennal sensitivity and behavioral threshold to odors in bumblebee workers. *Naturwissenschaften*, 94, 733-739.
- van Zweden, J. S. & d'Ettorre, P. (2010). Nestmate recognition in social insects and the role of hydrocarbons. *Insect hydrocarbons: biology, biochemistry and chemical ecology*, 11, 222-243.
- Whitehouse, M. E. & Jaffe, K. (1996). Ant wars: combat strategies, territory and nest defence in the leaf-cutting ant *Atta laevigata*. *Animal Behaviour*, 51, 1207-1217.
- Wilson, E. O. 1971: The Insect Societies. Harvard University Press, Cambridge, MA.
- Wilson, E. O. (1984). The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 16, 89-98.
- Wittwer, B., Hefetz, A., Simon, T., Murphy, L. E., Elgar, M. A., Pierce, N. E. & Kocher, S. D. (2017). Solitary bees reduce investment in communication compared with their social relatives. *Proceedings of the National Academy of Sciences*, 114, 6569-6574.

Figure 1 – Test arenas used in nestmate recognition trials (a) Bees were assayed in a partitioned glass container, which was cleaned of odours between trials and located between 6 and 8 metres from the nest. Each bee was given one minute to acclimatize before the petition was raised and the trial began. (b) Second-round assays were performed in a tube attached to the nest entrance, separated from the entrance by gauze, ensuring the test bees did not encounter an erroneous worker. Again the test bee was given one minute to acclimatize before the trial began.

Figure 2 – Variation in aggression and antennation frequency of focal bees towards nestmates and intruders in nest entrance trials. (a) Against nestmates aggression was low and similar between guards and foragers. Against intruders, guards were significantly more aggressive than foragers (Tukey's *post hoc* test, $p < 0.001$). (b) Foragers antennated on the antenna and abdomen of intruders significantly more often than the other treatments, indicative of recognition but displaying an unwillingness to fight (Tukey's *post hoc* test, $p = 0.0161$). N = 10 for each trial. (Fn – forager nestmate, Fnn – forager non-nestmate, Gn – guard nestmate, Gnn – Guard non-nestmate)

Figure 3 – Mean ($\pm$ standard error) sensilla density on antennomeres five, six, nine and ten of *T. carbonaria* foragers and guards. Consistent with most reported Hymenopteran, density increases distally along the antenna in all workers. However, density in guards is significantly higher than foragers, particularly on the most distal region of the antenna ($F_{(1,1)} = 5.0368$, $p = 0.0369$, $n = 10$). Bars are marked with standard error.

Figure 4 - Guards are consistently larger than foragers, as measured by intertegular distance. Mean size of guards is $1.188\text{mm} \pm 0.0273$, which is significantly greater than that of foragers, with a mean of $1.109\text{mm} \pm 0.0197$. White circles represent individual data points. N = 10.

Figure 5 – Head width of guards is also consistently larger than that of foragers. Mean head width of guards is $1.857\text{mm} \pm 0.0146$, which is significantly greater than that of foragers with a mean of 1.787 ± 0.0147 . White circles represent individual data points. N = 10.

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Wittwer, B;Elgar, MA

Title:

Cryptic castes, social context and colony defence in a social bee, *Tetragonula carbonaria*

Date:

2018-08-01

Citation:

Wittwer, B. & Elgar, M. A. (2018). Cryptic castes, social context and colony defence in a social bee, *Tetragonula carbonaria*. *ETHOLOGY*, 124 (8), pp.617-622. <https://doi.org/10.1111/eth.12765>.

Persistent Link:

<http://hdl.handle.net/11343/284125>