



Changes in maternal investment with climate moderate social behaviour in a facultatively social bee

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Abstract

Facultatively social species allow for empirical examination of the factors underlying evolutionary transitions between primitive and complex forms of sociality. Variation in climate along altitudinal and latitudinal gradients often influences social behaviour in these species. This facultative sociality has been well-documented in the ground-nesting bees, which have consistently greater social complexity in warmer, lower latitudes and altitudes. However, the potential combined effects of nesting biology and local climatic condition on social behaviour remain largely overlooked. To address this, we performed a long-term study on the facultatively social stem-nesting bee, *Ceratina australensis*, by assessing populations in three distinct climate zones over the course of three consecutive years. We compared nesting strategies across populations and found that the frequency of social nesting was stable with latitudinal changes in climate. Further, offspring survival was high for both solitary and social colonies, despite large fluctuations in the rate of parasitism across years, indicating that both nesting strategies are successful. However, maternal brood investment, which can strongly affect the social environment of a colony, was observed to fluctuate with climatic variation. Most notably, mothers produced small offspring of both sexes in the hottest driest years. Across all populations, social females were slightly larger than solitary females on average. As such, changes in maternal investment in response to annual and latitudinal climatic variation may be one of the many factors that ultimately determine that rate of social nesting. Variation in nest composition and climatic condition thus suggest that reproductive strategies in facultatively social stem-nesting bees may be influenced by climate constraints on maternal investment.

Significance statement

Climate alters the expression of social behaviour in many arthropod species but the relationship between climate and behaviour can vary broadly with taxa. For facultatively social species, theory generally predicts that sociality will increase in warmer climates, as longer brood rearing seasons provide opportunities for overlapping generations and cooperative brood care. However, little is known of the effect of compounding life-history factors, such as nesting biology. Here, we present a 3-year study on an incipiently social stem-nesting bee, *Ceratina australensis*. We find that the rate of sociality is stable across a broad latitudinal and climatic gradient, and we discuss the idea that nesting biology could potentially temper behavioural responses to climate. However, foundresses may alter their offspring investment in response to both annual weather and regional climatic variation, and this responsiveness could influence colony social behaviour.

Keywords Small carpenter bee · Stem-nesting bee · Social behaviour · Climate · Sex ratio · Parasitism

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Introduction

The transition in social complexity to obligate eusociality is a rare evolutionary phenomenon across the animal kingdom, but has occurred comparatively frequently in Hymenoptera. Obligate eusocial species function under a caste-based system, whereby the queen caste controls reproduction, and the

worker caste is sterile but performs all other tasks necessary for colony survival. The seemingly paradoxical, but repeated, evolution of a sterile worker caste in the Hymenoptera suggests that there are particular conditions under which otherwise restrictive barriers to the evolution of eusociality may be overcome (Rehan et al. 2012; Avila and Fromhage 2015). Empirical determination of the preconditions necessary for this transition is challenging given that most origins of eusociality are ancient (Brady et al. 2006; Moreau et al. 2006; Cardinal and Danforth 2011; Engel et al. 2016). However, species which demonstrate facultative social behaviour may be used to address this gap, as they offer models with which to examine both evolutionary transitions and the factors controlling the expression of flexible and non-obligate social phenotypes (Crespi 1996; Kocher and Paxton 2014; Rehan and Toth 2015; Shell and Rehan 2017). Studies on these facultatively social species are increasingly highlighting the importance of climatic and ecological factors in determining social phenotype (Reviewed by Purcell 2011; Toth and Rehan 2017).

Climatic temperature gradients have been strongly linked to changes in arthropod sociality (reviewed by Purcell 2011). Many arthropod species display higher levels of sociality in lower, warmer latitudes and altitudes (Purcell 2011). Warmer climates provide longer brood rearing seasons, which are thought to facilitate the development of sociality by improving the chances of generational overlap within colonies, and thereby the opportunities for cooperative brood care and reproductive division of labour (Michener 1974). This theory is well supported by comparative studies across ground-nesting bee species of the family Halictidae, in which populations demonstrate the expected increase in social nesting in lower latitudes and altitudes (e.g. Sakagami and Munakata 1972; Packer 1990; Eickwort et al. 1996; Miyanaga et al. 1999; Soucy and Danforth 2002; Zayed and Packer 2002; Field et al. 2010).

Many facultatively social species establish nests above ground. As these nests are inherently more exposed than those of ground-nesting taxa, climatic variation may be expected to elicit greater responsiveness from such species. For example, social phenotype in the spider genus *Anelosimus* covaries with a precipitation gradient rather than temperature (Purcell and Aviles 2008; Majer et al. 2013; Guevara and Avilés 2015). Bigger social groups form larger, sturdier nests that are better able to withstand heavy, damaging rainfall (Purcell and Aviles 2008). While the stem-nesting sweat bee *Megalopta genalis* had stable social behaviour across a steep precipitation gradient (Tierney et al. 2013), paper wasps (genus *Polistes*) also form nests aboveground, and the frequency of social nesting is associated with short-term temperature variability rather than with the average long-term climate (Sheehan et al. 2015). Flexible social responses to climate are also seen among various bee species. A study on two stem-nesting allodapine species (*Exoneura bicolor* and *E. richardsoni*) found that colony size increased in cooler altitudes (Schwarz et al. 1997), while a

study across a climatic range from temperate to subtropical on two other stem-nesting allodapine bees (*E. robusta* and *E. angophorae*) found no effect of climate on colony size (Cronin and Schwarz 1999). By contrast, the more widely researched ground-nesting sweat bees consistently demonstrate larger colony sizes in warmer climates (Sakagami and Munakata 1972; Packer 1990; Eickwort et al. 1996; Miyanaga et al. 1999; Soucy and Danforth 2002; Zayed and Packer 2002; Field et al. 2010). These studies thus suggest that there could be a phylogenetic divergence in the behaviour of these groups, or perhaps aboveground nesting species, and stem-nesting bees more narrowly, have different social responses to climate than those of ground-nesting bee species.

The social environment within colonies may also be modified by fine-scale changes in maternal investment as a response to climatic conditions. For instance, in the eusocial sweat bee, *Halictus ligatus*, mothers produced smaller female offspring during cool wet years, increasing the number of potential workers in the colony and allowing for greater monopolisation of reproduction by the queen (Richards and Packer 1995, 1996). By contrast, a comparison of two populations of the sweat bee, *Lasioglossum baleicum*, found that nests at shaded, cool sites were solitary, with larger, gynedestined offspring, while nests in unshaded, warmer sites were eusocial, with worker-sized brood (Hirata and Higashi 2008). These studies demonstrate that foundresses may alter their investment in response to both annual weather and regional climatic variation and that this may have a significant determining effect on colony social behaviour.

The social environment of a colony may also be affected by the timing of female offspring production and the number of female offspring reared. Hymenoptera can selectively fertilise their eggs and are thus able to control the sex of the offspring they produce. By investing in females, especially during the early breeding season, a foundress can effectively produce potential workers for her colony (Queller 1989; Gadagkar 1990). Variation in sex allocation with climate has been observed in two species of *Lasioglossum*, in which nests are female-biased and eusocial in warmer regions, and unbiased and solitary in colder regions (Sakagami and Munakata 1972; Cronin and Hirata 2003; Hirata and Higashi 2008). Because populations in the colder regions had time to produce only one brood a year, they lacked overlapping generations and the opportunity to make use of female helpers in the nest (Hirata and Higashi 2008). In comparison to these ground-nesting species, a study on two stem-nesting allodapine bees (*Exoneura robusta* and *E. angophorae*) found strongly female-biased brood sex ratios in multiple populations across a latitudinal gradient (Cronin and Schwarz 2001). Female-biased sex ratios are common in the allodapines and other stem-nesting bees, with daughters thought to act as alloparents in the event of foundress mortality (Watmough 1983; Maeta et al. 1992; Stark 1992; Sihag 1993; Schwarz et al. 2007).

Therefore, stable sex ratios across regional climate zones could be a feature of most facultatively social stem-nesting species.

Across facultatively social bees, research has focused on the theory that social nesting is a risk avoidance strategy to prevent nest failure due to parasitism or foundress mortality. Many facultatively social bee species benefit from reduced brood loss to parasitism in social nests by way of additional guards (e.g. Kukuk et al. 1998; Smith et al. 2003, 2007; Soucy et al. 2003; Zammit et al. 2008; Rehan et al. 2011; Mikát et al. 2016). In cases of foundress mortality, social nest brood may be protected against failure if alloparental care is provided by co-foundresses or adult siblings (Queller 1989; Gadagkar 1990). The caring for orphaned brood by other adults has been documented in hover wasps (Field et al. 2000), apoid wasps (Lucas and Field 2011), allodapine bees (Hogendoorn et al. 2001) and small carpenter bees (Mikát et al. 2017; Shell and Rehan 2018). The parasites themselves are subject to the climate, as are their host, and the combined activity of both host and parasite can affect the rate of offspring survival (Forrest and Chisholm 2017). These interactions can potentially have complex onward effects of sociality. For example, the paper wasp (*Polistes biglumis*) produces queen-like brood when under the combined pressures of cold temperatures and increased parasitism (Fucini et al. 2009). However, these insights are few, as studies investigating the incidence of social nesting and the relative cost/benefit ratio of social vs solitary reproduction rarely extend beyond 1 or 2 years. Detailed long-term assessments of facultatively social nesting, which consider variation in climatic condition, maternal investment and offspring survival over time and across a wide population distribution, are needed to more fully understand the relationship between ecology and the evolution of sociality.

Here, we present data from a 3-year study on the facultatively social, Australian small carpenter bee, *Ceratina (Neoceratina) australensis*, sampled from three populations, each within a distinct climate zone. Previous research on the social behaviour and nesting biology of this species has

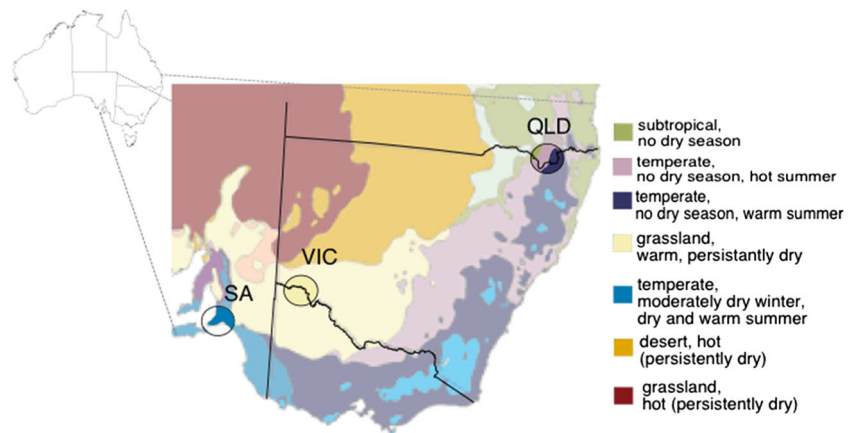
focused on a population in a subtropical region of Queensland, Australia. In this population, colonies are predominantly solitary, with a low frequency of incipiently social nests containing two or more adult females (Michener 1962; Rehan et al. 2010). Social nests are co-founded by sisters, who inherit their natal nest, and cooperatively reproduce and rear offspring to maturity (Rehan et al. 2014). The frequency of social nesting across years is thought to be stable in the population, regardless of changes in the rate of parasitism (Rehan et al. 2011). While previous research has focused on the Queensland region, *C. australensis* has since been found across the south-east of Australia in three genetically distinct populations (Dew et al. 2016). The overarching aim of this study was to determine if there was variation in social behaviour between these populations by comparing the following: (i) the frequency of social nesting, (ii) maternal investment in clutch size, offspring body size and sex ratio, and (iii) offspring survival. Based on the handful of extant studies on stem-nesting bees, we hypothesised that the frequency of social nesting and aspects of maternal investment would remain consistent across sites. Offspring survival was predicted to vary with annual weather patterns and regional climates due to corresponding changes in parasitism.

Methods

Sample collection

Ceratina australensis nests were collected from three populations in south-eastern Australia, located in three distinct climate zones (Fig. 1). Sampling at each site occurred in January in the summers of 2015, 2016 and 2017, which is approximately the middle of the brood rearing season. The plants used for nesting by *C. australensis* varied with site. In the subtropical-temperate Queensland (QLD) site (28.24°S, 152.09°E), nests were collected from roadside stands of giant fennel (*Ferula communis*). The site in Victoria (VIC; 34.15°S,

Fig. 1 Map showing the three sample sites within Australia. Sampled regions are circled. Climate is classified under the Köppen system, which is based on changes in vegetation type. Map is modified from the Bureau of Meteorology (<http://www.bom.gov.au>)



142.16°E) was a semi-arid riverine area, with nests found in dark sago-weed (*Plantago drummondii*), while nests in the South Australia (SA) site (34.94°S, 138.50°E) were collected from searocket (*Cakile maritima*) on coastal dunes. All nests were collected in the early morning or late evening to ensure capture of all colony members. Upon collection, nest entrances were sealed with masking tape and placed on ice until processing.

Data collection

During processing, nests were split lengthwise, and all colony contents were recorded, including dead and parasitised brood. As nesting substrate clearly identified source population, these data could not be recorded blind. The head width, measured as the distance between the furthest distances to the outer edges of the compound eyes, was recorded for all adult bees and pupae and used as a proxy for total body size (Rehan et al. 2010). Colonies were classified by their stage in brood development following Rehan and Richards (2010a). ‘Founding’ nests were those without brood or provisions; ‘active’ nests were those in the process of producing and provisioning pollen balls and eggs; and ‘full brood’ nests were those where all brood cells had been completed. Full brood nests were specifically identified by the presence of an offspring that had matured to a larva at least one-third the size of its pollen ball in the final cell. Lastly, ‘mature brood’ nests were those in which some of the brood were late stage pupae alongside newly enclosed offspring.

Clutch size was determined by counting all of the brood cells, including those that were parasitised, or had pollen balls but no offspring yet, in full brood nests only, as these nests represent a mother’s total reproductive investment. Nests were deemed social if there were two or more adult females present during the full brood or active brood stages, as these relatively early stages prevent misclassification due to the presence of mature offspring later in the season. At the VIC site, body size measurements for social females were only obtained in 2017 and limited to individuals from three nests. Therefore, we focused only on the QLD and SA populations for our comparisons of adult female size between social and solitary nests. Per capita brood production was calculated from clutch size for all full brood nests. Offspring sex ratio (r) was calculated for each nest based on the sex of pupae and enclosed adult offspring ($r = \text{number of male offspring} / \text{total number of offspring}$). As brood were frozen in the field for transport to the University of New Hampshire, USA, immature offspring (eggs and larvae) could not be reared to maturity and a complete sex ratio was not determined for some nests. The sex, size and brood cell position of offspring was measured; as brood cells are provisioned sequentially, these metrics allowed for an assessment of maternal investment over the total course of brood production. Only active or full brood nests were used for brood cell comparisons, as brood cell position cannot be determined in mature brood nests once offspring

enclose. The number of live offspring was calculated in full brood nests by excluding brood cells where offspring had been parasitised, or were otherwise dead or missing. This allowed a proportion of live offspring out of the complete clutch size to be calculated for each nest assessed.

Climate comparison

In order to gain an understanding of the conditions experienced by the bees during the course of the study, we gathered detailed weather data for each site and year. Data were sourced from the Bureau of Meteorology (<http://www.bom.gov.au>) from weather stations within 13 km of each collection site. For the QLD site, temperature data were obtained from the Warwick station (28.21°S, 152.10°E) and precipitation from the Warwick alert station (28.21°S, 152.03°E). VIC temperature data were obtained from the Mildura airport station (34.24°S, 142.09°E) and precipitation from the Irymple station (34.23°S, 142.15°E). SA temperature and precipitation data were both obtained from the Adelaide airport station (34.95°S, 138.52°E). We then calculated cumulative climatic statistics across a window spanning September 1st to January 31st, which covered the start of the brood rearing season through nest collection each year. The cumulative maximum temperature per day was calculated for days 25 °C and over, as these are days that are warm enough for bees to forage (Rehan et al. 2011; Fig. 2a). The cumulative precipitation (mm) per day was also calculated, as bees do not forage when it is raining (Fig. 2b).

Statistical analyses

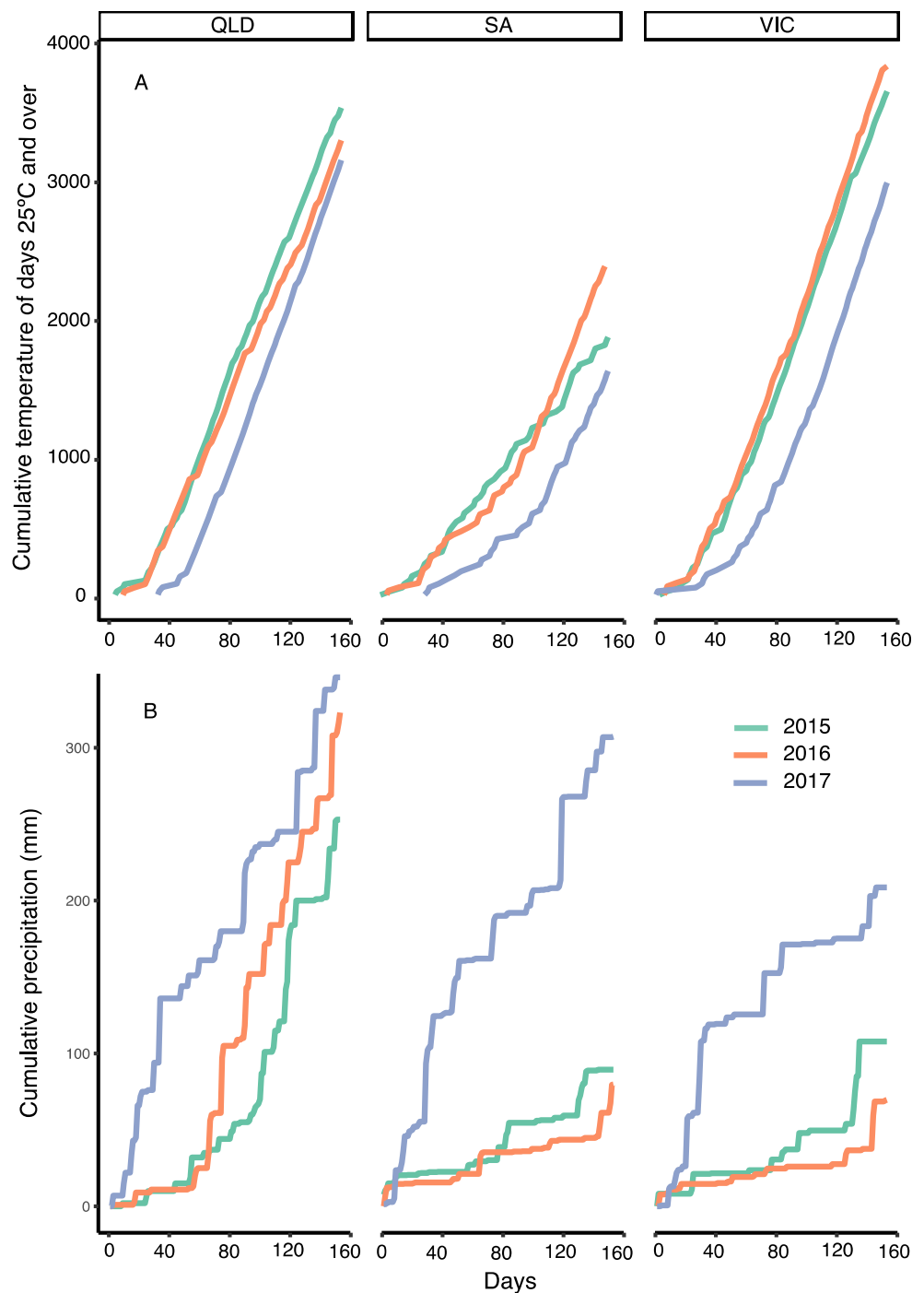
Analyses were performed in R v.3.3.1. Chi-square tests were used to compare the frequency of occurrences of social nesting and parasitism between site and year. All significant Chi-square tests were followed by pairwise comparisons of proportions, with Bonferroni corrected p values reported, to determine where the differences occur. All other relationships in the data were assessed by two-way ANOVAs. All models initially included the predictors of site, year and nesting strategy (i.e. social or solitary). Models were then evaluated by stepwise comparison of the Akaike information criterion (AIC), and significant results from the final models were explored by Tukey HSD post hoc analysis.

Results

Cumulative climate data and colony social structure

The cumulative temperature of days above 25 °C was lowest in SA for all 3 years and peaked in VIC in 2015 and 2016 (Fig. 2a). Across all sites, 2017 was the coolest year and had the highest cumulative precipitation (Fig.

Fig. 2 Cumulative temperature (a) and precipitation (b) for each site. Days are counted from the start of spring to mid-summer (September 1 to January 30) each year. The highest cumulative temperature was in VIC 2016, while 2017 was the year of highest cumulative precipitation at all sites



2b). Peak cumulative precipitation was recorded in QLD in 2017 and 2016.

A summary of the number of nests collected from each site in each year is shown in Table 1.

There were no social nests found in VIC during 2015, while the most social nests were collected from SA during 2016, which was much higher than the other years at that site (Table 1). This variation in the number of social nests from SA was significant ($\chi^2_2 = 18.05$, $P < 0.001$), with 2016 having a higher proportion of nests than 2015 ($P < 0.001$).

However, 2017 did not statistically differ from the preceding years ($P = 0.140$; $P = 0.947$). Social nesting also differed between years in VIC overall based on Chi-square analysis ($\chi^2_2 = 6.38$, $P = 0.041$), but the pairwise comparison of proportions post hoc analysis between each year found no significant differences ($P \geq 0.170$). The QLD site did not significantly differ between years from an average of 4.34% social nesting ($\chi^2_2 = 2.39$, $P = 0.303$).

The head width of a total of 841 adult females was measured, as a proxy for body size. Both year and site were

Table 1 Number of *Ceratina australensis* nests collected in each site per year

| Site | Year | Total number of nests | Number of AB/FB nests | Number of social nests | Percentage social |
|------|------|-----------------------|-----------------------|------------------------|-------------------|
| QLD | 2015 | 139 | 56 | 2 | 3.6 |
| | 2016 | 126 | 87 | 4 | 4.6 |
| | 2017 | 96 | 50 | 5 | 10.0 |
| SA | 2015 | 313 | 154 | 3 | 1.9 |
| | 2016 | 252 | 147 | 23 | 15.6 |
| | 2017 | 62 | 26 | 2 | 7.7 |
| VIC | 2015 | 32 | 20 | 0 | 0.0 |
| | 2016 | 39 | 30 | 3 | 10.0 |
| | 2017 | 40 | 15 | 4 | 26.7 |

The total number of nests collected, the number of those in the reproductively active brood (AB)/full brood (FB) stages and the number of social nests are shown. Percentage social is the number of social nests out of the total AB/FB nests. Social nests were found at a low frequency across all sites

significant predictors of adult female body size (year: $F_2 = 24.9$, $P < 0.001$; site $F_2 = 3.65$, $P = 0.027$). Females were significantly smaller in 2015 than 2016 and 2017 ($N_{2015} = 325$, $N_{2016} = 345$, $N_{2017} = 171$; $P < 0.001$) and significantly smaller in VIC compared to QLD ($N_{VIC} = 310$, $N_{QLD} = 80$; $P = 0.024$). There were no significant differences in female size between the other years ($P = 0.934$) or sites ($P \geq 0.155$). On average, social females in QLD and SA were larger than their solitary conspecifics (Wilcoxon: $N_{QLD} = 70$, $N_{SA} = 691$, $W = 16,266$, $P < 0.001$; Fig. 3). This analysis excluded the VIC site as females were significantly smaller at this site, and there was a limited sample size of measured social females.

Maternal investment

Clutch size varied from one to a maximum of 13, with an average of 6.1 ± 0.2 s.e. offspring per nest. Clutch size did not differ significantly between social and solitary nests

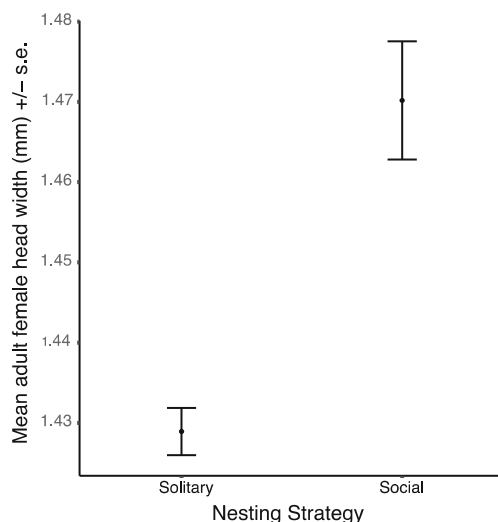


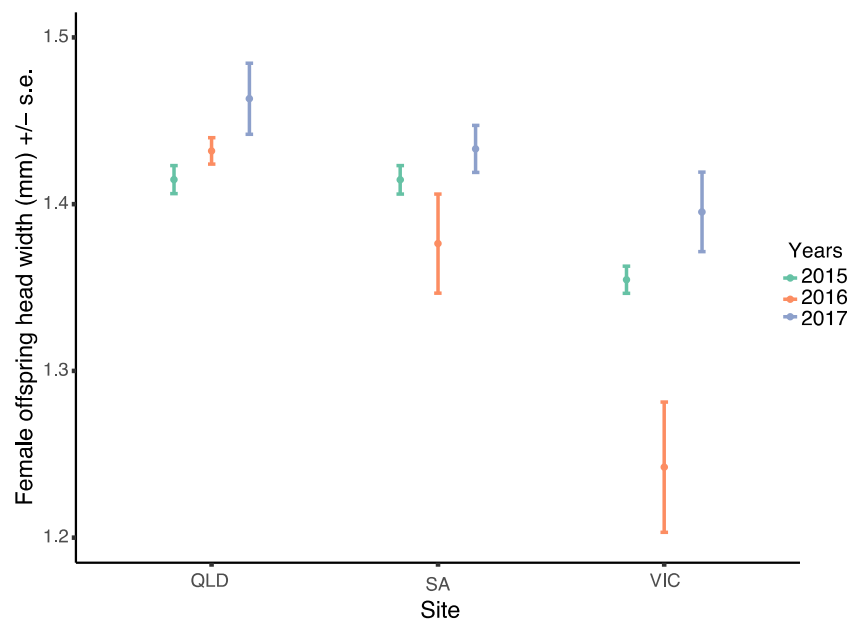
Fig. 3 Comparison of the size of adult females between social and solitary colonies. Data are pooled from the QLD and SA populations. Social females are on average larger than solitary individuals ($P < 0.001$)

($N_{social} = 10$, $N_{solitary} = 206$; $F_1 = 0.39$, $P = 0.533$), but there were significant differences in clutch size between site and year ($F_4 = 5.06$, $P < 0.001$). Post hoc analysis indicated that the clutch size of colonies in QLD was smaller in 2017 than 2016 ($N_{2016} = 26$, mean = 4.1 ± 0.5 s.e.; $N_{2017} = 29$, mean = 7.4 ± 0.6 ; $P < 0.001$). Comparison among sites revealed that QLD in 2016 likewise had smaller clutch sizes than during 2015 in SA ($N = 43$; mean = 6.5 ± 0.5 ; $P = 0.004$) and VIC ($N = 15$; mean = 7.6 ± 0.8 ; $P = 0.028$). No other sites or seasons had significantly different clutch sizes ($P \geq 0.056$).

Per capita brood production (PCBP) varied significantly with nesting strategy ($F_1 = 12.73$, $P < 0.001$), social nests having a lower PCBP ($N = 8$, mean = 2.5 ± 0.3) than solitary nests ($N = 206$, mean = 6.0 ± 0.2 , $P < 0.001$). PCBP also differed significantly among sites and years ($F_4 = 5.23$, $P < 0.001$). Post hoc analysis showed that in 2017, the QLD site had significantly lower PCBP (mean = 3.9 ± 0.5) than observed in 2016 (mean = 7.3 ± 0.7 ; $P = 0.002$). Colonies from QLD in 2017 also has low PCBP when compared to the SA (mean = 6.4 ± 0.5 ; $P = 0.045$) and VIC sites in 2015 (mean = 7.6 ± 0.8 ; $P = 0.006$). All other sites and seasons did not significantly differ in PCBP ($P \geq 0.065$).

The head widths of a total of 130 female and 92 male offspring were measured. Offspring size varied between sites and years for both male ($F_4 = 2.77$, $P = 0.033$) and female offspring ($F_4 = 3.20$, $P = 0.015$; Fig. 4), but not between solitary and social nests ($P \geq 0.239$). In general, female offspring in VIC ($N = 23$) was smaller than other sites (QLD: $N = 58$, SA: 49). Post hoc analysis found that offspring in VIC were significantly smaller during 2016 than all years in QLD ($P < 0.001$; Fig. 4), as were VIC offspring in 2015 compared to QLD 2017 ($P = 0.019$). VIC offspring from 2016 were also smaller than VIC offspring in 2017 ($P = 0.001$) and SA offspring from 2015 and 2017 ($P < 0.001$; Fig. 4). Across years, male offspring tended to be smaller in VIC ($N = 10$, mean = $1.32 \text{ mm} \pm 0.014$) than QLD ($N = 25$, mean = $1.40 \text{ mm} \pm 0.012$; $P = 0.004$) and SA ($N = 57$, mean = $1.38 \text{ mm} \pm 0.007$;

Fig. 4 Mean female offspring size per site. The smallest offspring at each site were produced in 2015 in QLD and 2016 in SA and VIC



$P = 0.022$). Male offspring in QLD and SA did not significantly differ in size ($P = 0.404$). For male offspring, yearly differences in size were driven by SA in 2016, which had smaller brood sizes than SA in 2015 ($P = 0.005$) and QLD in 2016 ($P = 0.008$). There was also no change in offspring size among brood cells for either female (Kruskal-Wallis: $\chi^2_7 = 6.30$, $P = 0.505$) or male offspring ($\chi^2_5 = 10.49$, $P = 0.062$).

Sex was scored for a total of 240 female and 165 male offspring, allowing us to calculate sex ratio for 150 colonies. Sex ratio did not vary with year or between solitary and social nests, but it did vary with site ($F_2 = 7.08$, $P = 0.001$) with colonies in VIC ($N = 25$) and QLD ($N = 50$) being significantly more female biased than SA ($N = 77$, $P = 0.016$; $P = 0.004$, respectively; Fig. 5). The sex ratio of VIC and QLD nests was not significantly different ($P = 0.972$). The colony level sex ratio was driven by sex allocation of the first brood cell, which was significantly female biased in both QLD and VIC colonies ($\chi^2_1 = 19.6$, $P < 0.001$; $\chi^2_1 = 10$, $P = 0.002$; Table 2). The sex ratio for all other brood cells in QLD and VIC nests, as well as all brood cells in the SA nests, did not significantly differ from an unbiased sex ratio ($P > 0.157$; Table 2).

Offspring survival

Solitary vs social nesting strategy was not a significant predictor of offspring survival ($F_1 = 1.63$, $P = 0.203$), but the number of live offspring was significantly different among sites and years ($F_4 = 10.17$, $P < 0.001$). Post hoc analysis found that differences among years were predominantly driven by the QLD site. In 2016, QLD had more live offspring than QLD in 2015 and 2017, SA 2016 and VIC 2016 ($P \leq 0.005$). By contrast, in 2017, QLD had fewer live offspring than all years in SA ($P = 0.037$). SA 2015 nests also had more

live offspring than VIC 2016 ($P = 0.046$). However, when the proportion of live offspring surviving out of the entire clutch was considered, there was no significant differences among sites ($F_2 = 1.66$, $P = 0.193$), years ($F_2 = 1.44$, $P = 0.240$) or nesting strategies ($F_1 = 0.062$, $P = 0.804$). On average, the proportion of live offspring was greater than 75% at all sites.

While there was no statistical difference in the overall proportion of colonies parasitised between social and solitary nests ($N_{\text{social}} = 52$, $N_{\text{solitary}} = 930$, $\chi^2_3 = 6.83$, $P = 0.078$), the rates of parasitism varied significantly among sites ($N_{\text{QLD}} = 356$, $N_{\text{SA}} = 625$, $N_{\text{VIC}} = 110$, $\chi^2_2 = 8.87$, $P = 0.012$) and years ($N_{2015} = 481$, $N_{2016} = 417$, $N_{2017} = 193$, $\chi^2_2 = 34.73$, $P < 0.001$). Post hoc pairwise comparison of the proportion of parasitised brood between all sites and years showed that VIC in 2015 had a significantly higher rate of parasitism than SA in 2015 ($P < 0.001$) and QLD in both 2015 and 2016 ($P < 0.001$; $P = 0.002$; Fig. 6). QLD nests in 2017 were significantly more parasitised than 2015 and 2016 ($P \leq 0.001$), while SA nests in 2015 were significantly less parasitised than either 2016 or 2017 ($P \leq 0.01$; Fig. 6).

Discussion

Our study of the facultatively social stem-nesting bee (*Ceratina australensis*) found a low frequency of social nesting across three populations collected across a considerable latitudinal and climatic gradient (Table 1), consistent with research on two other stem-nesting bees (Cronin and Schwarz 1999). However, contrary to our predictions based on that study, maternal investment was observed to vary significantly among years and sites. Changes in maternal investment, such as the size and number of females produced, may ultimately

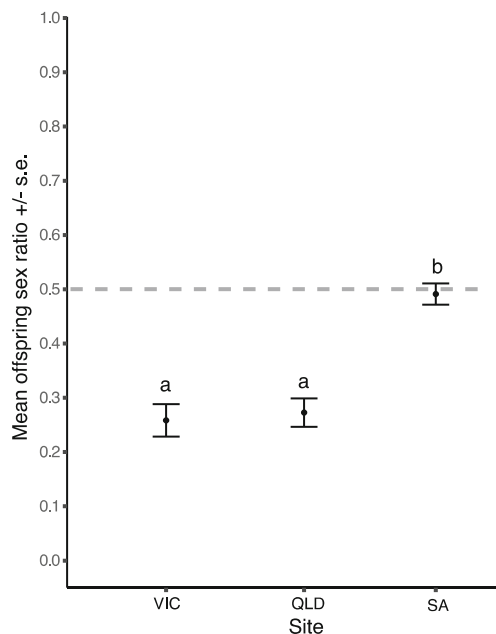


Fig. 5 Mean offspring sex ratio of colonies from each site. Dotted line represents an unbiased sex ratio of 50% male. Both VIC and QLD have strongly female-biased sex ratios. Letters above site means indicate significant differences from post hoc analyses ($p < 0.05$)

influence colony social environment. Thereby, our results suggest that changes in maternal investment driven by regional climate could affect the expression of sociality in this species. Notably, social females were on average larger than their solitary conspecifics, suggesting that adult female body size may influence nesting strategy (Fig. 3). Clutch size, PCBP and offspring body size varied widely across sites and years. Offspring body size of both males and females was smaller overall in semi-arid VIC, the hottest and driest site (Fig. 4). Interestingly, small offspring of both sexes were produced during the hottest and driest years. Female offspring were significantly smaller in the hottest driest year in VIC (Figs. 2 and 4). Male offspring were also small in hot dry years, with significantly smaller male offspring produced in the hottest driest year in SA (Fig. 2). Summer conditions in Australia can be severe, and floral resources required for brood

provisions may be greatly reduced during particularly hot and dry spells. While there was no difference in the size of female offspring between brood cell positions, sex ratios were significantly female biased in the first brood cell of nests from VIC and QLD but not SA (Fig. 5, Table 2). This variation in female-biased sex allocation among sites may indicate site-specific differences in social nest formation (Seeger 1983). Despite fluctuations in brood parasitism rates, offspring survival was relatively high, around 75% on average, across all populations.

Sociality across latitudinal gradients

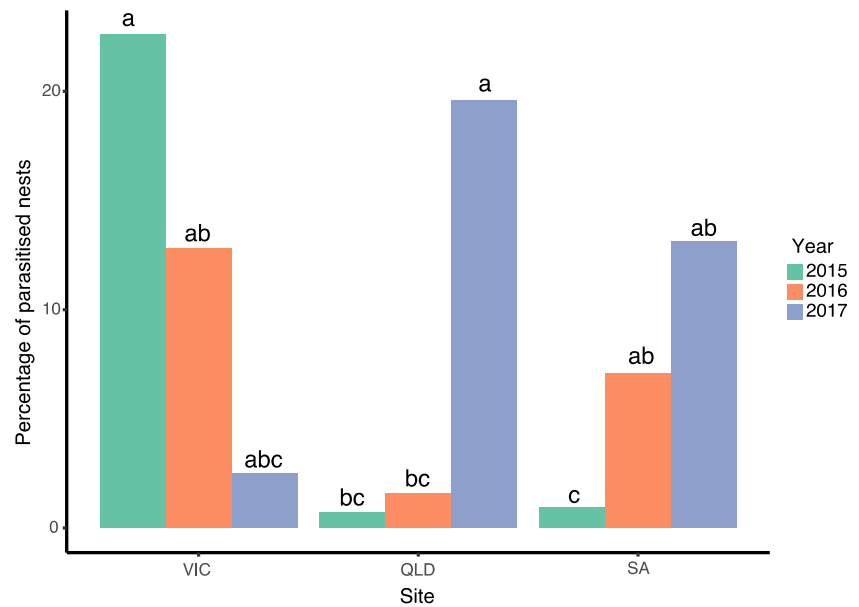
Although there was subtle annual variation in rates of social nesting among our sites, consistent low frequencies of social nesting in all three populations of *C. australensis* suggest that the incidence of sociality is at least partially independent of climate. While the study was based over 3 years, and longer than many similar studies, it is possible that these data are too few to detect a correlation that would be evident from a long-term dataset across multiple decades. But if there is an effect of social nesting we have not detected, it is certainly much subtler than that of the ground-nesting species previously studied. While this may appear surprising, stability of social nesting across climate variation has been observed in previous research on stem-nesting bees (Cronin and Schwarz 1999, 2001; Tierney et al. 2013). This is distinct from ground-nesting bees, which often demonstrate clear variation in sociality across similar latitudinal and climatic gradients (e.g. Packer 1990; Miyanaga et al. 1999; Zayed and Packer 2002). The observed variation in social nesting, however, did not show a direct association with our cumulative temperature and precipitation variables (Fig. 2). This supports the findings by Rehan et al. (2011), which examined the effects of weather variation on the QLD population over 2 years. Stable social behaviour across regional climates may be common to the carpenter bees (Apidae: Xylocopinae) or perhaps stem-nesting bees more broadly. The subterranean nests of ground-nesting species (Halictidae) are relatively protected

Table 2 The number of male and female offspring in each brood cell position

| Brood cell | QLD | | | | VIC | | | | SA | | | |
|------------|-----|---|-------|-------------------|-----|---|-------|--------------|----|----|-------|-------|
| | ♀ | ♂ | Total | P | ♀ | ♂ | Total | P | ♀ | ♂ | Total | P |
| 1 | 25 | 2 | 27 | <i>< 0.001</i> | 10 | 0 | 10 | <i>0.002</i> | 23 | 20 | 43 | 0.647 |
| 2 | 11 | 7 | 18 | 0.346 | 4 | 6 | 10 | 0.527 | 14 | 22 | 36 | 0.182 |
| 3 | 5 | 3 | 8 | 0.480 | 4 | 2 | 6 | 0.414 | 8 | 8 | 16 | 1.000 |
| 4 | 4 | 4 | 8 | 1.000 | 6 | 2 | 8 | 0.157 | 7 | 4 | 11 | 0.366 |
| 5+ | 12 | 4 | 16 | 0.572 | 6 | 2 | 8 | 0.564 | 6 | 8 | 14 | 0.449 |

Departures from the expected sex ratio of 1:1 were assessed via Chi-square, finding significant female bias in the 1st brood cell of nests in QLD and VIC. Significant *P* values are shown in italics

Fig. 6 Percentage of parasitised nests in each site and year. The percentage of parasitism varied widely between site and year. Columns that do not share a common letter are significantly different from post hoc analyses ($p < 0.05$)



against day-to-day meteorological variation (Cane 1991) and are largely buffered against even extreme events such as forest fires and hurricanes (Cane 1997; Cane and Neff 2011). In comparison, the nests of stem-nesting bees are relatively exposed. The walls of the stem likely offer some insulation, but nests still experience a large variation in temperature, precipitation and wind. As stem-nesting species face a much more complex variety of conditions, this could explain why we have not observed a straight forward behavioural response to climate in the stem-nesting bees studied so far. Notably, the one stem-nesting bee of the Halictidae studied in this manner showed stable social behaviour across a large precipitation gradient (Tierney et al. 2013), suggesting that nesting behaviour may be more influential than phylogeny in explaining geographic variation in sociality.

Maternal investment changes with climate

While the frequency of social nesting was consistent among sites, there were changes in maternal investment with climate that may ultimately, but indirectly, alter colony and population level sociality, in concert with other factors. The size of female offspring in *C. australensis* is associated with temperature and precipitation, with small offspring occurring under hot dry conditions (Figs. 2 and 4). Changes in offspring size mediated by climate are known to alter the relative production of gyne and worker destined brood in other hymenopteran colonies (Richards and Packer 1996; Hirata and Higashi 2008; Fucini et al. 2009; Brito et al. 2013; Holland and Bourke 2015; Molet et al. 2017). Variation in worker body size with climate can also affect the enforcement of reproductive hierarchies, as can be seen in the ground-nesting bee, *Halictus ligatus*, where the production of small female offspring led to more strongly eusocial colonies, with low rates of worker reproduction

(Richards and Packer 1996). While social nestmates in *C. australensis* do not display size dimorphism (Rehan et al. 2010), our finding that social adult females were on average slightly larger than their solitary conspecifics indicates that foundress size may play a role in determining social or solitary nest establishment. Social females also tend to be larger in the species *Ceratina calcarata*, and studies on this species have shown a significant correlation between social female size and female quality (Shell and Rehan 2018). Female size could likewise be an indication of quality in *C. australensis*. Nonetheless, the size difference between social and solitary females indicates that offspring size variation with climate could be one of several of factors influencing the number of social females in a population. Annual variation in climatic condition may thus be an indirect factor influencing the expression of social phenotype through changing maternal brood investment.

Colony social environment may also be modified by the sex ratio of the offspring produced. The first brood cell is the first provisioned by the mother and hence contains the oldest offspring. Intriguingly, the first brood cell was female biased in the VIC and QLD sites, consistent with sex allocation patterns observed in the social nests of other *Ceratina* species. In these species, socially nesting mothers may give their first daughter a relatively small pollen provision, in which cases she will develop into a very small adult, dwarfed by her sisters (Sakagami and Maeta 1977, 1984, 1995; Johnson 1988; Rehan and Richards 2010b; Vickruck 2010). This ‘dwarf eldest daughter’ forages for her siblings to provide the essential food needed prior to overwintering and can also take on alloparental roles in the event of foundress mortality (Rehan and Richards 2010a; Lawson et al. 2016; Mikát et al. 2017; Shell and Rehan 2018). While the female offspring produced in the first brood cell are not smaller than their siblings in

C. australensis, the conspicuous female bias could represent a pre-cursor of similar helping behaviour.

Very few studies have compared the sex allocation of stem-nesting bees across populations and climate zones, but the existing research suggests that female-biased sex ratios are conserved (Cronin and Schwarz 2001; Schwarz 1994). The unbiased sex ratio of nests in SA is unusual, given that a female biased first brood cell is common to both VIC and QLD and across many *Ceratina* species (Sakagami and Maeta 1977, 1984, 1995; Johnson 1988; Rehan and Richards 2010b; Vickruck 2010). In facultatively social insects, a female-biased sex ratio is thought to facilitate the evolution of worker behaviour (Hamilton 1964; Trivers and Hare 1976; Gardner and Ross 2013). Therefore, the observed fine-scale change in sex allocation could be indicative of long-term trends of differentiation in social behaviour between these populations.

Benefits to social nesting

Previous work on *C. australensis* has suggested that the low frequency of social nesting in this species is a risk avoidance strategy in response to variable offspring survivorship, likely due to parasitism intensity (Rehan et al. 2011, 2014). Parasitism is commonly cited as an ecological constraint selecting for social nesting, as the presence of multiple adults allows one to act as a guard in the nest while others forage (Chenoweth et al. 2007; Zammit et al. 2008; Mikát et al. 2016). While the rate of parasitism varied widely throughout our study (Fig. 6), the proportional offspring survival was remarkably consistent. Females may respond to high parasitism rates by producing more brood. Alternatively, conditions that favour brood productivity in *C. australensis* may also favour parasite reproduction, counteracting any overall productivity benefit. This has been observed in the solitary bee, *Osmia iridis*, which increases brood provisioning in warmer temperatures but simultaneously suffers greater offspring losses to more active parasites (Forrest and Chisholm 2017). It is also possible that social nests of *C. australensis* only have an advantage in times of extreme parasite load, not detected during our study.

Interestingly, social females were found to be larger than solitary individuals on average, and this may hint at a physiological factor underlying social nesting (Fig. 3). This study and previous work identified no PCBP benefits to social nesting (Rehan et al. 2011, 2014). However, larger females are potentially better able to survive overwintering, forage for food, and provision a large brood, and may consequently have greater lifetime fitness (Rehan and Richards 2010b; Durant et al. 2016; Mikát et al. 2017; Shell and Rehan 2018). This may also be advantageous for the subordinate female in social nests, who avoids the energy and risk expense

involved with foraging (Rehan and Richards 2010b; Shell and Rehan 2018).

Conclusions

Although climate does not seem to directly affect the frequency of social nesting in stem-nesting bees studied to date, it does appear to be a determining factor of maternal investment strategies in *C. australensis*. Production of small female offspring during dry, warm conditions may be one factor influencing the annual variation in the number of social females. Moreover, the differences in sex ratio with site indicate that there are differences in colony social environment among populations. However, the tendency for on average slightly larger and presumably higher quality females to nest socially indicates that there may be a selective advantage maintaining this behaviour. As seen in *C. australensis*, climate moderated variation in maternal investment and subsequent variation in colony demography, may be key factors contributing to the maintenance of facultative sociality in stem-nesting bees.

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References

- Avila P, Fromhage L (2015) No synergy needed: ecological constraints favor the evolution of eusociality. *Am Nat* 186:31–40. <https://doi.org/10.1086/681637>
- Brady SG, Sipes S, Pearson A, Danforth BN (2006) Recent and simultaneous origins of eusociality in halictid bees. *Proc R Soc B Biol Sci* 273:1643–1649. <https://doi.org/10.1098/rspb.2006.3496>
- Brito DV, Da Silva Nunes RA, Pequeno PA et al (2013) Differential environmental effects on caste allocation in two Amazonian *Melipona* bees. *Apidologie* 44:666–672. <https://doi.org/10.1007/s13592-013-0215-8>
- Cane JH (1991) Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *J Kansas Entomol Soc* 64: 406–413
- Cane JH (1997) Violent weather and bees: populations of the Barrier Island endemic, *Hesperapis oraria* (Hymenoptera: Melittidae) survive a category 3 hurricane. *J Kansas Entomol Soc* 70:73–75
- Cane JH, Neff JL (2011) Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biol Conserv* 144:2631–2636. <https://doi.org/10.1016/j.biocon.2011.07.019>
- Cardinal S, Danforth BN (2011) The antiquity and evolutionary history of social behavior in bees. *PLoS One* 6:e21086. <https://doi.org/10.1371/journal.pone.0021086>
- Chenoweth LB, Tierney SM, Smith JA, Cooper SJB, Schwarz MP (2007) Social complexity in bees is not sufficient to explain lack of

- reversions to solitary living over long time scales. *BMC Evol Biol* 7: 246. <https://doi.org/10.1186/1471-2148-7-246>
- Crespi BJ (1996) Comparative analysis of the origins and losses of eusociality: causal mosaics and historical uniqueness. In: Martins EP (ed) *Phylogenies and the comparative method in animal behavior*. Oxford University Press, New York, pp 253–287
- Cronin AL, Hirata M (2003) Social polymorphism in the sweat bee *Lasioglossum (Evyllaesus) baleicum* (Cockerell) (Hymenoptera, Halictidae) in Hokkaido, northern Japan. *Insect Soc* 50:379–386. <https://doi.org/10.1007/s00040-003-0693-1>
- Cronin AL, Schwarz MP (1999) Latitudinal variation in the life cycle of allodapine bees (Hymenoptera; Apidae). *Can J Zool* 77:857–864. <https://doi.org/10.1139/z99-040>
- Cronin AL, Schwarz MP (2001) Latitudinal variation in the sociality of allodapine bees (Hymenoptera: Apidae): sex ratios, relatedness and reproductive differentiation. *Aust J Entomol* 49:1–16
- Dew RM, Rehan SM, Schwarz MP (2016) Biogeography and demography of an Australian native bee *Ceratina australensis* (Hymenoptera: Apidae) since the last glacial maximum. *J Hymenopt Res* 49:25–41
- Durant DR, Berens AJ, Toth AL, Rehan SM (2016) Transcriptional profiling of overwintering gene expression in the small carpenter bee, *Ceratina calcarata*. *Apidologie* 47:572–582. <https://doi.org/10.1007/s13592-015-0402-x>
- Eickwort GC, Eickwort JM, Gordon J, Eickwort MA (1996) Solitary behavior in a high altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 38:227–233. <https://doi.org/10.1007/s002650050236>
- Engel MS, Barden P, Riccio ML, Grimaldi DA (2016) Morphologically specialized termite castes and advanced sociality in the early cretaceous. *Curr Biol* 26:522–530. <https://doi.org/10.1016/j.cub.2015.12.061>
- Field J, Paxton RJ, Soro A, Bridge C (2010) Cryptic plasticity underlies a major evolutionary transition. *Curr Biol* 20:2028–2031. <https://doi.org/10.1016/j.cub.2010.10.020>
- Field J, Shreeves G, Sumner S, Casiraghi M (2000) Insurance-based advantage to helpers in a tropical hover wasp. *Nature* 404:869–871. <https://doi.org/10.1038/35009097>
- Forrest JRK, Chisholm SPM (2017) Direct benefits and indirect costs of warm temperatures for high-elevation populations of a solitary bee. *Ecology* 98:359–369. <https://doi.org/10.1002/ecy.1655>
- Fucini S, Di Bona V, Mola F et al (2009) Social wasps without workers: geographic variation of caste expression in the paper wasp *Polistes biglumis*. *Insect Soc* 56:347–358. <https://doi.org/10.1007/s00040-009-0030-4>
- Gadagkar R (1990) Evolution of eusociality: the advantage of assured fitness returns. *Philos Trans R Soc B Biol Sci* 329:17–25
- Gardner A, Ross L (2013) Haplodiploidy, sex-ratio adjustment, and eusociality. *Am Nat* 181:E60–E67. <https://doi.org/10.1086/669147>
- Guevara J, Avilés L (2015) Ecological predictors of spider sociality in the Americas. *Glob Ecol Biogeogr* 24:1181–1191. <https://doi.org/10.1111/geb.12342>
- Hamilton WD (1964) The genetical evolution of social behaviour. II *J Theor Biol* 7:17–52. [https://doi.org/10.1016/0022-5193\(64\)90039-6](https://doi.org/10.1016/0022-5193(64)90039-6)
- Hirata M, Higashi S (2008) Degree-day accumulation controlling allopatric and sympatric variations in the sociality of sweat bees, *Lasioglossum (Evyllaesus) baleicum* (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 62:1239–1247. <https://doi.org/10.1007/s00265-008-0552-1>
- Hogendoorn K, Watiniasih NL, Schwarz MP (2001) Extended alloparental care in the almost solitary bee *Exoneurella eremophila* (Hymenoptera: Apidae). *Behav Ecol Sociobiol* 50:275–282. <https://doi.org/10.1007/s002650100357>
- Holland JG, Bourke AFG (2015) Colony and individual life-history responses to temperature in a social insect pollinator. *Funct Ecol* 29: 1209–1217. <https://doi.org/10.1111/1365-2435.12480>
- Johnson MD (1988) The relationship of provision weight to adult weight and sex ratio in the solitary bee, *Ceratina calcarata*. *Ecol Entomol* 13:165–170. <https://doi.org/10.1111/j.1365-2311.1988.tb00344.x>
- Kocher SD, Paxton RJ (2014) Comparative methods offer powerful insights into social evolution in bees. *Apidologie* 45:289–305. <https://doi.org/10.1007/s13592-014-0268-3>
- Kukuk PF, Ward SA, Jozwiak A (1998) Mutualistic benefits generate an unequal distribution of risky activities among unrelated group members. *Naturwissenschaften* 85:445–449. <https://doi.org/10.1007/s001140050528>
- Lawson SP, Ciaccio KN, Rehan SM (2016) Maternal manipulation of pollen provisions affects worker production in a small carpenter bee. *Behav Ecol Sociobiol* 70:1891–1900. <https://doi.org/10.1007/s00265-016-2194-z>
- Lucas ER, Field J (2011) Assured fitness returns in a social wasp with no worker caste. *Proc R Soc London B Biol Sci* 278:2991–2995. <https://doi.org/10.1098/rspb.2011.0128>
- Maeta Y, Sugiura N, Goubara M (1992) Patterns of offspring production and sex allocation in the small carpenter bee, *Ceratina flavipes* SMITH (Hymenoptera, Xylocopinae). *Japanese J Entomol* 60: 175–190
- Majer M, Agnarsson I, Svenning JC, Bilde T (2013) Social spiders of the genus *Anelosimus* occur in wetter, more productive environments than non-social species. *Naturwissenschaften* 100:1031–1040. <https://doi.org/10.1007/s00114-013-1106-6>
- Michener CD (1962) The genus *Ceratina* in Australia, with notes on its nests (Hymenoptera: Apoidea). *J Kansas Entomol Soc* 35:414–421
- Michener CD (1974) *The social behavior of the bees*. Belknap Press of Harvard University Press, Cambridge
- Mikát M, Černá K, Straka J (2016) Major benefits of guarding behavior in subsocial bees: implications for social evolution. *Ecol Evol* 6:6784–6797. <https://doi.org/10.1002/ece3.2387>
- Mikát M, Franchino C, Rehan SM (2017) Sociodemographic variation in foraging behavior and the adaptive significance of worker production in the facultatively social small carpenter bee, *Ceratina calcarata*. *Behav Ecol Sociobiol* 71:135. <https://doi.org/10.1007/s00265-017-2365-6>
- Miyayama R, Maeta Y, Sakagami SF (1999) Geographical variation of sociality and size-linked color patterns in *Lasioglossum (Evyllaesus) apristum* (Vachal) in Japan (Hymenoptera, Halictidae). *Insect Soc* 46:224–232. <https://doi.org/10.1007/s000400050138>
- Molet M, Péronnet R, Couette S, Canovas C, Doums C (2017) Effect of temperature and social environment on worker size in the ant *Temnothorax nylanderii*. *J Therm Biol* 67:22–29. <https://doi.org/10.1016/j.jtherbio.2017.04.013>
- Moreau CS, Bell CD, Vila R, Bruce Archibald S (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Pierce Source Sci New Ser* 312:101–104
- Packer L (1990) Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range. *Behav Ecol Sociobiol* 27:339–344. <https://doi.org/10.1007/BF00164004>
- Purcell J (2011) Geographic patterns in the distribution of social systems in terrestrial arthropods. *Biol Rev* 86:475–491. <https://doi.org/10.1111/j.1469-185X.2010.00156.x>
- Purcell J, Avilés L (2008) Gradients of precipitation and ant abundance may contribute to the altitudinal range limit of subsocial spiders: insights from a transplant experiment. *Proc R Soc B Biol Sci* 275: 2617–2625. <https://doi.org/10.1098/rspb.2008.0582>
- Queller DC (1989) The evolution of eusociality: reproductive head starts of workers. *Evolution* 86:3224–3226. <https://doi.org/10.1073/pnas.86.9.3224>
- Rehan SM, Leys R, Schwarz MP (2012) A mid-cretaceous origin of sociality in xylocopine bees with only two origins of true worker castes indicates severe barriers to eusociality. *PLoS One* 7:e34690. <https://doi.org/10.1371/journal.pone.0034690>

- Rehan SM, Richards MH (2010a) Nesting biology and subsociality in *Ceratina calcarata* (Hymenoptera: Apidae). *Can Entomol* 142:65–74. <https://doi.org/10.4039/n09-056>
- Rehan SM, Richards MH (2010b) The influence of maternal quality on brood sex allocation in the small carpenter bee, *Ceratina calcarata*. *Ethology* 116:876–887. <https://doi.org/10.1111/j.1439-0310.2010.01804.x>
- Rehan SM, Richards MH, Adams M, Schwarz MP (2014) The costs and benefits of sociality in a facultatively social bee. *Anim Behav* 97:77–85. <https://doi.org/10.1016/j.anbehav.2014.08.021>
- Rehan SM, Richards MH, Schwarz MP (2010) Social polymorphism in the Australian small carpenter bee, *Ceratina (Neoceratina) australensis*. *Insect Soc* 57:403–412. <https://doi.org/10.1007/s00040-010-0097-y>
- Rehan SM, Schwarz MP, Richards MH (2011) Fitness consequences of ecological constraints and implications for the evolution of sociality in an incipiently social bee. *Biol J Linn Soc* 103:57–67. <https://doi.org/10.1111/j.1095-8312.2011.01642.x>
- Rehan SM, Toth AL (2015) Climbing the social ladder: the molecular evolution of sociality. *Trends Ecol Evol* 30:426–433. <https://doi.org/10.1016/j.tree.2015.05.004>
- Richards MH, Packer L (1995) Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). *Can J Zool* 73:933–941
- Richards MH, Packer L (1996) The socioecology of body size variation in the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae) *Oikos* 77:68–76
- Sakagami S, Maeta Y (1995) Task allocation in artificially induced colonies of a basically solitary bee *Ceratina (Ceratinidia) okinawana*, with a comparison of sociality between *Ceratina* and *Xylocopa* (Hymenoptera, Anthophoridae, Xylocopinae). *Japanese J Entomol* 63:115–150
- Sakagami SF, Maeta Y (1977) Some presumably presocial habits of Japanese *Ceratina* bees, with notes on various social types in Hymenoptera. *Insect Soc* 24:319–343. <https://doi.org/10.1007/BF02223784>
- Sakagami SF, Maeta Y (1984) Multifemale nests and rudimentary castes in the normally solitary bee *Ceratina japonica* (Hymenoptera: Xylocopinae). *J Kansas Entomol Soc* 57:639–656
- Sakagami SFS, Munakata M (1972) Distribution and bionomics of a transpalaeartic eusocial halictine bee, *Lasioglossum (Evylaeus) calceatum*, in northern Japan, with reference to its solitary life cycle at high altitude. *J Fac Sci Hokkaido Univ Ser VI Zool* 18:411–439
- Schwarz MP, Richards MH, Danforth BN (2007) Changing paradigms in insect social evolution: insights from halictine and allodapine bees. *Annu Rev Entomol* 52:127–150. <https://doi.org/10.1146/annurev.ento.51.110104.150950>
- Schwarz MP, Silberbauer LX, Hurst PS (1997) Intrinsic and extrinsic factors associated with social evolution in allodapine bees. In: Choe JC, Crespi B (eds) *The evolution of social behaviour in insects and arachnids*. Cambridge University Press, Cambridge, pp 476–498
- Seger J (1983) Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature* 301:59–62. <https://doi.org/10.1038/301059a0>
- Sheehan MJ, Botero CA, Hendry TA, Sedio BE, Jandt JM, Weiner S, Toth AL, Tibbetts EA (2015) Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol Lett* 18:1057–1067. <https://doi.org/10.1111/ele.12488>
- Shell WA, Rehan SM (2017) Behavioral and genetic mechanisms of social evolution: insights from incipiently and facultatively social bees. *Apidologie* 49:13–30. <https://doi.org/10.1007/s13592-017-0527-1>
- Shell WA, Rehan SM (2018) The price of insurance: costs and benefits of worker production in a facultatively social bee. *Behav Ecol* 29:204–211. <https://doi.org/10.1093/beheco/axx146>
- Sihag RC (1993) Behaviour and ecology of the subtropical carpenter bee, *Xylocopa fenestrata* F. 8. Life cycle, seasonal mortality, parasites and sex ratio. *J Apic Res* 32:109–114. <https://doi.org/10.1080/00218839.1993.11101295>
- Smith AR, Wcislo WT, O'Donnell S (2003) Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 54:14–21. <https://doi.org/10.1007/s00265-003-0589-0>
- Smith AR, Wcislo WT, O'Donnell S (2007) Survival and productivity benefits to social nesting in the sweat bee *Megalopta genalis* (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 61:1111–1120. <https://doi.org/10.1007/s00265-006-0344-4>
- Soucy SL, Danforth BN (2002) Phylogeography of the socially polymorphic sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Evolution* 56:330–341
- Soucy SL, Giray T, Roubik DW (2003) Solitary and group nesting in the orchid bee *Euglossa hyacinthina* (Hymenoptera, Apidae). *Insect Soc* 50:248–255. <https://doi.org/10.1007/s00040-003-0670-8>
- Stark RE (1992) Sex ratio and maternal investment in the multivoltine large carpenter bee *Xylocopa sulcatipes* (Apoidea: Anthophoridae). *Ecol Entomol* 17:160–166. <https://doi.org/10.1111/j.1365-2311.1992.tb01174.x>
- Tierney SM, Fischer CN, Rehan SM, Kapheim KM, Wcislo WT (2013) Frequency of social nesting in the sweat bee *Megalopta genalis* (Halictidae) does not vary across a rainfall gradient, despite disparity in brood production and body size. *Insect Soc* 60:163–172. <https://doi.org/10.1007/s00040-012-0280-4>
- Toth AL, Rehan SM (2017) Molecular evolution of insect sociality: an eco-evo-devo perspective. *Annu Rev Entomol* 62:419–442. <https://doi.org/10.1146/annurev-ento-031616-035601>
- Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insects. *Science* 191:249–263.
- Vickruck J (2010) The nesting biology of *Ceratina* (Hymenoptera: Apidae) in the Niagara region: new species, nest site selection and parasitism. Brock University, St. Catharines, Ontario, Canada
- Watmough RH (1983) Mortality, sex ratio and fecundity in natural populations of large carpenter bees (*Xylocopa* spp.) *J Anim Ecol* 52:111–125
- Zammit J, Hogendoorn K, Schwarz MP (2008) Strong constraints to independent nesting in a facultatively social bee: quantifying the effects of enemies-at-the-nest. *Insect Soc* 55:74–78. <https://doi.org/10.1007/s00040-007-0972-3>
- Zayed A, Packer L (2002) Genetic differentiation across a behavioural boundary in a primitively eusocial bee, *Halictus poeyi* Lepeletier (Hymenoptera, Halictidae). *Insect Soc* 49:282–288. <https://doi.org/10.1007/s00040-002-8315-x>