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RESEARCH ARTICLE

Social polymorphism in the Australian small carpenter bee, *Ceratina* (*Neoceratina*) *australensis*

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Abstract The bee tribe Ceratinini provides important insights into the early stages of sociality. Many arthropods exhibit behaviours precursory to social life, including adult longevity, parental care, nest loyalty and mutual tolerance, yet the origins of social behaviour are few. Here we describe the biology of a facultatively social bee, *Ceratina* (*Neoceratina*) *australensis*, which exhibits all of the preadaptations for successful group living, yet presents ecological and behavioural characteristics that seemingly disfavour frequent colony formation. This species is socially polymorphic with both solitary and social nests collected in sympatry. Social colonies consist of two foundresses, one contributing both foraging and reproductive effort and the second which remains at the nest as a passive guard. Cooperative nesting provides no overt reproductive benefits over solitary nesting in this population, although brood survival tends to be greater in social colonies. Maternal longevity, subsociality and bivoltine nesting phenology in this species favour colony formation, while dispersal habits and offspring longevity may inhibit more frequent social nesting in this and other ceratinines.

Keywords Ceratinini · Facultative social behaviour · Reproductive differentiation · Small carpenter bees · *Ceratina*

Introduction

The origin of eusociality from solitary antecedents is one of the major transitions in evolution (Maynard Smith and Szathamáry, 1995). The highly eusocial termites, ants, wasps and corbiculate bees all evolved sociality >65 million years ago and exemplify end stages rather than origins of social behaviour (Thorne et al., 2000; Engel and Grimaldi, 2005; Wenzel, 1990; Michener, 2007). Scrutinizing these highly social clades to infer the nature of the earliest insect societies is difficult, if not impossible, because transitional stages no longer exist, and solitary ancestors are hypothetical starting points with only derived highly eusocial end points for study. Understanding transitions from solitary to social life requires a group of closely related taxa possessing both social and non-social species, ideally with recent and repeated origins of sociality. The resulting contrasts would allow us to tease out the genetic, life history and environmental factors that promoted or constrained the origins of sociality.

Compared to the advanced eusocial insects, more recent and labile social evolution is found in the halictine and allodapine bees (Schwarz et al., 2007), and these primitively eusocial taxa have provided insights into the evolutionary steps from solitary to social life. Extensive behavioural data and robust molecular phylogenies have revealed that evolutionary origins of eusociality are few, with three origins and 12 losses of eusociality in the halictines (Danforth, 2002) and a single origin of sociality with no reversion to purely solitary life in allodapines (Chenoweth et al., 2007).

Early studies (Michener, 1974; Wilson, 1971) suggested that sociality had evolved within the bee tribe Allodapini and that its sister tribe, Ceratinini, was largely solitary. This suggested that extant allodapines may contain some inter-

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esting contrasts that could be used to infer early stages in the evolution of true sociality, whereas ceratinines represented an origin of extended mother-brood contact, with sporadic tolerance of adult daughters by still-reproductive mothers. However, it is now known that sociality is an ancestral trait for Allodapini, with no known losses of sociality (Chenoweth et al., 2007), whereas an increasing number of studies indicate that multi-female nesting during brood rearing may be widespread among Ceratinini (Sakagami and Maeta, 1977, 1987, 1995; Rehan et al., 2009).

All ceratinines studied to date are subsocial (sensu Michener, 1969; Wilson, 1971; Tallamy and Wood, 1986), with prolonged maternal care and mother–offspring interactions (Sakagami and Maeta, 1977; Michener, 1990; Rehan et al., 2009; Rehan and Richards, 2010). In addition, some species are socially polymorphic, with both solitary and social nests in the same population (Sakagami and Maeta, 1987; Michener, 1985). Solitary nests are attended by a single adult female while social colonies usually contain two, but occasionally three to four, adult females (Michener, 1990; Rehan et al., 2009). Reproductive division of labour and social polymorphism is recurrent among the Old World subgenera, *Neoceratina* (Rehan et al., 2009), *Ceratinidia* (reviewed in Michener, 1985; Rehan et al., 2009), *Pithitis* (Rehan et al., 2009) and possibly *Ctenoceratina* (Daly, 1988). However, most subgenera and the vast majority of species have not been studied. The ceratinines may therefore provide comparative material that can help elucidate the origins of multi-female nesting as well as reproductive differentiation among nestmates, in the way that allodapines were once thought to provide.

Ceratina are well represented on all continents except Australia where there is a single described species, *C.* (*Neoceratina*) *australensis*. The life history and social potential of *C. australensis* was previously described, based on monthly sampling from July 1958 through February 1959 comprising a total of 38 nests, with a single nest in which brood were being reared by two females (Michener, 1962). In the absence of larger sample sizes, the life cycle, developmental rate of immatures and the significance of two-female associations remain speculative. Here we use nest collections of *C. australensis* over a period of 20 months, covering winter, spring and summer periods to investigate colony phenology, social nesting, reproductive hierarchies and brood productivity. We use these data to discuss factors that influence colony formation and behavioural preadaptations in incipiently social taxa.

Methods

A total of 612 *C. australensis* nests were collected from dead broken stems of giant fennel (*Ferula communis*) in and around the shire of Warwick in the warm temperate zone of southern Queensland, Australia (28°13′S 152°02′E, 480 m elevation). Fennel stalks were found along rural roadsides adjacent to grain and cattle farms in Warwick and surrounding areas. Nests were collected prior to 0700 hours to ensure that bees had not commenced flight activity for the day, and so that all nest occupants would be present. Stems were broken at the base and the nest entrances sealed with masking tape for transport on ice to the laboratory, where they were stored at 5°C until examined. Nests were split lengthwise and contents recorded, including number of brood cells, number of live brood, developmental stages of brood, number and location of adult bees, and overall nest appearance. Nest lengths were measured using digital calipers (accuracy ± 0.01 mm). Collections were undertaken at four times during the year: winter (July 2007 and 2008), early spring (October 2007 and 2008), late spring (December 2007 and 2008) and late summer (February 2008 and 2009).

Nests were categorized according to the developmental stages of Daly (1966) and Rehan et al. (2009). *Hibernacula* contain faecal pellets or pollen residue with darkened interior walls from the previous breeding season and may contain one to six adult bees. *Founding* nests contain eggs, larval provisions or brood cells and are formed in newly excavated pith. *Active brood* nests contain pollen masses with eggs or small larvae. In full brood nests, the cell closest to the nest entrance contains a larva or pupa. Only full brood nests were used to evaluate the number of live brood and clutch size (the number of brood cells in the nest). *Mature brood* nests contain callow offspring and adult bees, but no pollen provisions or immature offspring. In addition to these stages, nests were categorized as new versus reused. *New nests* have clean walls devoid of pollen stains and faecal pellets while *reused nests* have darkened walls with pollen and/or faecal stains from previous provisioning and brood rearing in that twig.

Brood were removed from the nest and reared in the laboratory at a temperature ranging between 23 and 25°C in 200 μl microcentrifuge tubes with an air hole inserted in the lid. Each immature was observed daily to determine the number of days spent in each of the 18 developmental stages previously identified for ceratinine bees (Daly, 1966; Rehan et al., 2009).

Adult females were assessed in terms of body size and reproductive status. Head width was measured across the widest part of the head to the outer margins of both compound eyes. Wing lengths were measured along the costal vein from the base of the wing to the proximal tip of the stigma. Wing length and head width were linearly correlated ($r = 0.812$, $n = 129$, $P < 0.0001$). In addition, females were weighed using a Mettler analytical balance (accuracy 0.001 mg). Live weight and head width were linearly correlated ($r = 0.787$, $n = 94$, $P < 0.0001$), therefore head width was used as a proxy for body size for adult females. Wing wear was scored to assess foraging effort (Cartar, 1992). Bees with no nicks or tears on the apical margins of both forewings received a wing wear score of zero, and bees with the apical margin of both forewings completely worn to shreds received a wing wear score of five. Adult females were dissected to determine reproductive status. Ovary size was measured as the sum of the lengths of the three largest terminal oocytes (accuracy ± 0.01 mm). Insemination status was determined by the presence or absence of sperm in the spermatheca.

In this study, solitary nests contain a single foundress and social colonies contain two foundresses. Social nests were conservatively identified when two adult females were found within nests with reproductive activity (active and full brood nests). However, hibernacula, founding nests and mature brood nests were not recorded as social colonies as these represent pre- and post-reproductive assemblages, which could potentially disperse prior to reproduction.

Statistical analyses

Descriptive statistics, goodness-of-fit tests, *t* tests, ANOVA and resampling statistics were carried out using SAS version 9.1. Data were assessed for normality and when response variables were not normally distributed; continuous measures were replaced with ranks for non-parametric statistics. Measures were combined across samples for all statistical analyses.

Results

Frequency of social nesting

Of 612 nests collected over two years, 262 were reproductive (active and full brood) nests, and 36 (14%) of these contained two adult females with the remainder containing a single adult female. Solitary and social nests were found in neighbouring fennel stalks and were indistinguishable except for the number of adult females inside. Social colonies were collected in early spring, late spring and summer. Collections of social nests showed that they were at stages similar to those of solitary nests collected at the same time (Table 1).

Colony cycle

Ceratina australensis immatures develop from egg to adulthood in about 34 days (Table 2), and the maximum age difference between youngest and oldest offspring within a given nest was 21 days. Therefore, the maximum time required to complete a brood should be about 55 days. Based on nest collections (Table 1) and brood developmental rates (Table 2), the seasonal phenology of the species is depicted in Fig. 1 and described below.

Table 1 Sample size and developmental stage of *Ceratina australensis* nests collected in Warwick, Queensland

Collection period	Nest category	Solitary nests				Social nests			
		Nest appearance		Status of foundresses		Nest appearance		Status of foundresses	
		New	Reused	Unworn	Worn	New	Reused	Unworn	Worn
July (winter)	H	25	42	82	32	–	–	–	–
October (early spring)	FN	88	23	99	12	–	–	–	–
	AB	35	11	37	8	0	7	7	7
	FB	0	0	–	–	–	–	–	–
	MB	0	0	–	–	–	–	–	–
December (early summer)	FN	10	11	16	5	–	–	–	–
	AB	26	7	23	10	0	6	8	4
	FB	47	2	31	11	0	4	4	4
	MB	1	4	1	3	–	–	–	–
February (summer)	FN	70	5	65	10	–	–	–	–
	AB	40	8	40	7	1	16	24	10
	FB	33	17	26	16	0	2	1	3
	MB	32	39	25	7	–	–	–	–

– not applicable

H hibernacula, *FN* founding nest, *AB* active brood nest, *FB* full brood nest, *MB* mature brood nest

Table 2 Developmental rates of immature brood of *Ceratina australensis*

Stage	Mean (days)	SD (days)	*n*
Egg			
Egg	3.00	1.41	4
1/3–2/3 pb	2.10	1.00	10
2/3–7/8 pb	1.10	0.23	10
1 × pb	1.69	0.50	13
Larva			
1.5 × pb	1.44	0.50	18
2 × pb	1.92	1.63	24
Small bit pb	2.15	0.95	27
Fully grown larva	2.11	1.50	36
Prepupae	4.29	2.38	61
Pupa			
White	1.39	0.58	84
Pink	1.52	0.58	89
Red	1.61	1.29	83
Brown	2.06	0.96	94
Black	2.01	0.63	98
1/4	1.22	0.25	85
1/2	0.99	0.25	92
3/4	1.25	0.96	90
Fully pigmented	1.84	1.54	93
Total	33.73	1.69	1011

Eggs take on average 3 days to hatch and begin feeding on pollen mass (*pb* pollen mass)

Larval stages describe larva length compared to pollen mass (1/3, full grown larva)

Prepupae consume their entire pollen mass and defecate becoming more slender than younger larvae

Pupal stages (white–black) describe eye pigmentation changes

Pupal stages (1/4, fully pigmented) describe body pigmentation observations, 1/4 pigmented through fully pigmented. Once fully pigmented, the bee sheds one final moult becoming an adult

In winter (July collections), all nests found were hibernacula, about one-third being newly constructed and two-thirds being reused nests. Hibernacula contained on average two adult females per nest (range 1–6 females). No males or immatures were found in hibernacula.

In early spring (October collections), all nests collected were founding nests and active brood nests, so provisioning and oviposition of brood were at an early stage. The majority of spring nests were newly constructed, with about 25% (41/164) being reused. By early summer (December collections), most (92/118, 78%) nests were in the active and full brood stages, but there were also a few founding (21/118, 18%) and mature brood (5/118, 4%) nests as well. As in early spring, the majority of early summer nests were of new construction.

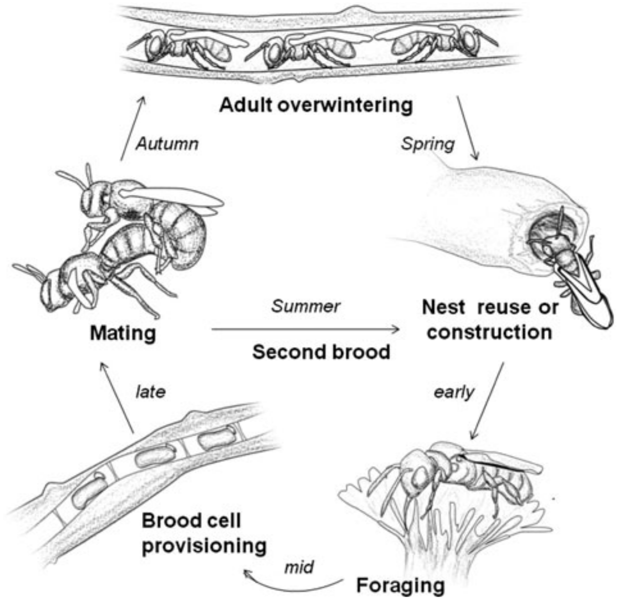

Fig. 1 Bivoltine colony cycle of *Ceratina australensis* in southern Queensland, Australia. Females overwinter (May–August) in hibernacula. In early spring (September–October), females disperse and found nests or reuse hibernacula. Mid-spring (October–November) females forage and provision brood cells. Late spring (November–December) provisioned brood mature in the nest and eclose as callow adults. Offspring emerge and mate at this time. Following emergence of the spring brood, a second brood is initiated in early summer (January). Nest construction or reuse and brood cell provisioning span the summer months (January–February). Come autumn (March–April), the second brood offspring eclose. Callow offspring remain at the natal nest or emerge and re-nest, founded twigs for overwintering

The few founding nests collected in early summer likely represent early production of a second brood. This second brood was produced mainly in midsummer (February collections) as shown by the abundance of founding and active brood nests collected (Table 1). These cannot have been first brood nests because, as noted above, it takes less than two months to complete a brood. The proportions of new and reused nests were similar in summer and late spring collections, i.e. the proportion of newly constructed nests was similar for first and second brood (Fisher's exact test, $P = 0.46$).

Overwintering females (July collections) were a mix of unworn (72%) and worn (28%) individuals (Table 1). Worn females in hibernacula must have been foragers during the previous summer and must therefore have been first brood females produced in spring. Females that were unworn most likely were second brood females produced over the previous summer. Therefore, hibernacula contained both first and second brood females.

The considerations above suggest that there are two brood production periods, Brood 1 and Brood 2. Early spring collections revealed that 12% of nesting females were heavily worn (wing wear score >3), even though their nests were only in the founding and active brood stages. This implies that worn females were nesting for the second time, whereas unworn females were nesting for the first time. Likewise, 25% of nesting females from summer collections were heavily worn, so again these must have been re-nesting while unworn females were nesting for the first time. In other words, individual females followed one of the following nest phenologies: females could produce their first brood in spring and then a second one in summer, or, if they emerge in late spring, produce a first brood in summer and then a second one in spring after overwintering. Since the proportions of unworn and worn females did not vary between new and reused nests ($\chi_1^2 = 2.25$, $P = 0.32$), there was no correlation between female age and nest reuse patterns.

Maternal care and longevity

Mothers inspect brood during their development. At the time of nest opening females were found inside brood cells amongst loose pith partitions and inspecting immature bees in 7/245 (3%) of attended active and full brood nests. Mothers were found inspecting innermost and outermost brood cell positions. However, 238/245 (97%) mothers were found guarding the nest facing backwards with their abdomen blocking the entrance in active and full brood nests and all cell septa were found intact in nests when the mother was discovered at the nest entrance. This suggests that mothers inspect brood cells on occasion, but must reconstruct brood cell partitions following inspection.

Females are long lived and nest loyal as evinced by adult females found in 99% (155/157) of active brood, 86% (90/105) of full brood, 47% (36/76) of mature brood and 87% (530/612) of all nests. The mean period from commencement of brood rearing to maturation of the brood is 34 days (Table 1). Therefore, adult females were likely to have lived for at least one year prior to collection with their complete brood, considering the duration of overwintering and brood production.

Reproductive hierarchies in social colonies

In the absence of observation nests we examined reproductive differentiation and its possible determinants using colony census and dissection data from females collected in active and full brood nests. Solitary females were used as a point of comparison to determine the possible roles of females in social colonies.

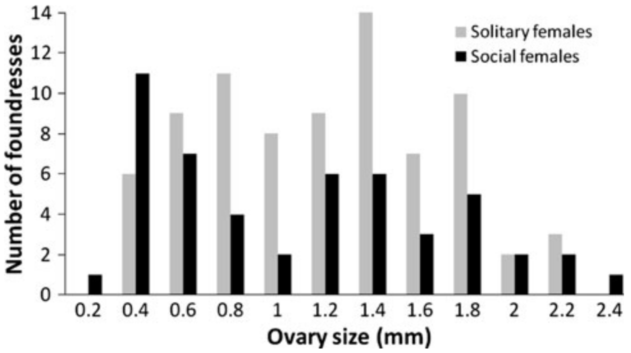

Fig. 2 Comparison of reproductive status among *Ceratina australensis* females from active and full brood nests

First, reproductive differentiation between nestmates in social nests was addressed by examining the distribution of reproductive development in social and solitary nests (Fig. 2). Given the range of ovary sizes across the population as a whole, we asked if reproductive differentiation between social females was greater than would be expected among randomly drawn pairs of solitary females. To do this we used a Monte Carlo resampling technique (Sokal and Rohlf, 1995). The mean absolute difference in ovarian sizes between 25 pairs of females in social colonies was calculated. We then randomly selected 25 pairs of females without replacement from the solitary nests and calculated their mean differences in ovary size. This procedure was repeated 1,000 times to produce a null distribution of differences among randomly selected solitary females to which we compared the observed mean difference between females in social colonies. Only four of the 1,000 simulated mean ovary size differences were greater than that observed in the social colonies, indicating that the difference in ovary size was greater in social colonies than would be expected by chance. Two-sample *t* tests comparing ovary sizes of solitary females with first ovary size-ranked social females revealed no difference ($t_{79,\ 25} = -0.934$, $P = 0.17$), while solitary and second ovary size-ranked social females were significantly different ($t_{79,\ 25} = 3.44$, $P = 0.02$).

Second, we addressed whether ovary size scales with body size independently of social interactions. To do this we compared head width to ovary size in solitary females from reproductive (active and full brood) nests. There was no relationship between body size and ovary size ($r^2 = 0.03$, $n = 79$, $P = 0.102$). Given the lack of body-size scaling of ovary size in solitary females, we compared body size and ovary size in social nests. For social colonies, we ranked individuals according to ovary size and compared absolute body size between first (1.48 ± 0.07 mm) and second (1.46 ± 0.07 mm) ovary size-ranked social females in the population. This showed no significant difference (paired *t* test, $t_{25} = 1.43$, $P = 0.16$). We then ranked social individuals according to body size and ovary size and tested these two ranks for independence for all samples combined and found no dependence between ranks (Fisher's exact test, $P = 0.24$).

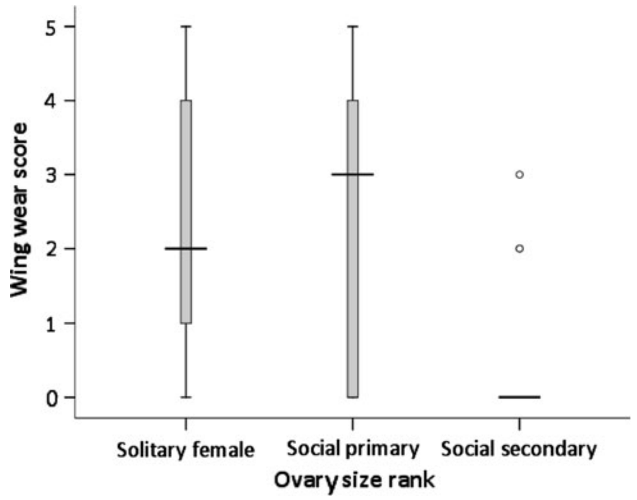

Fig. 3 *Box plots* of wing wear scores to ovary size ranks. *Circles* represent outliers

Thirdly, we examined ovary size as a function of wing wear. We tested whether wing wear differed between first and second ovary size-ranked females in social colonies. There was a significant difference (Fig. 3; paired *t* test, $t_{25} = 5.36$, $P < 0.0001$) in wing wear between primary (3.31 ± 0.93 mm) and secondary (0.48 ± 0.35 mm) ovarian size-ranked social females. Two sample *t* tests again revealed that secondary ovary size-ranked social females had significantly less wing wear than solitary (2.47 ± 1.68 mm) females ($t_{25,\ 79} = -6.41$, $P < 0.0001$), but solitary and primary ovarian size-ranked social females did not differ from each other ($t_{79,\ 25} = -0.01$, $P = 0.50$).

The significant relationship among ovary size rank and wing wear prompted additional exploration of wing wear as a predictor of reproductive differentiation. First, wing wear variation between nestmates was addressed by categorizing females as having either the greater or lesser wing wear than their nestmate. Much like the ovary size analyses above, we examined wing wear as a function of ovary size. We tested whether ovary size differed between primary and secondary wing wear score-ranked females in social colonies. There was a significant difference in ovary size between primary (1.94 ± 0.58 mm) and secondary (1.00 ± 0.40 mm) wing wear-ranked social females (paired *t* test, $t_{25} = 6.93$, $P < 0.001$). Two sample *t* tests revealed that secondary wing wear-ranked social females had significantly smaller ovaries than solitary (1.56 ± 0.62 mm) females ($t_{25,\ 79} = -3.30$, $P = 0.001$), but solitary and primary wing wear-ranked social females did not differ from each other ($t_{25,\ 79} = 1.7$, $P = 0.13$).

We then addressed whether wing wear scales with body size independently of social interactions. To do this we compared head width to wing wear in solitary females from reproductive (active and full brood) nests. There was no correlation between body size and wing wear ($r = 0.08$, $n = 79$, $P = 0.48$). Given the lack of body-size scaling of wing wear in solitary females, we compared relative wing wear and body size in social nests. For social colonies we ranked individuals according to wing wear and compared absolute body size among solitary (1.47 ± 0.07 mm), primary (1.48 ± 0.07 mm) and secondary (1.45 ± 0.07 mm) wing wear-ranked social females in the population. There was no significant difference in body size between primary and secondary wing wear-ranked social females (paired *t* test, $t_{25} = 1.65$, $P = 0.11$). Two sample *t* tests further confirmed there was no difference in body size between solitary and primary wing wear-ranked social females ($t_{79,\ 25} = 0.10$, $P = 0.92$) or solitary and secondary wing wear-ranked social females ($t_{79,\ 25} = 1.64$, $P = 0.11$).

Overall, colony census and dissection data from adult females collected in reproductive nests indicate that: (i) there is bimodality in ovary size and wing wear among social females, (ii) body size is a poor indicator of both wing wear and ovary size in social colonies, (iii) females with larger ovaries tend to have greater wing wear, and (iv) solitary females are similar to social first ovary size-ranked female in both ovary size and wing wear patterns.

Nest architecture and brood productivity

Of the 612 nests collected, 204 or 33% were reused and 408 or 67% were newly founded nests. Nest lengths ranged from 9 to 245 mm. New nests were 80.3 ± 31.9 mm and reused nests 83.2 ± 29.6 mm in length, and there was no significant difference between these means ($t_{201,\ 121} = 0.811$, $P = 0.42$). Reused nests were soiled throughout, suggesting that nests were not lengthened prior to reuse.

To determine the effect of nest reuse on reproductive success, we compared the number of brood cells provisioned in new and reused full brood nests. There was no significant difference in clutch size between new (5.61 ± 2.96) and reused (5.42 ± 3.0) nests ($t_{61,\ 30} = 1.11$, $P = 0.27$). In addition, there was no significant difference in the number of live brood ($t_{61,\ 30} = 0.41$, $P = 0.68$) between new and reused complete nests. This suggests that females which rear brood in reused nests are no more fecund than those rearing brood in new nests.

Social colonies were found predominantly in reused nests (35/36 colonies) suggesting that cohabiting females remain in previously used nests rather than co-found new nests. There was no significant difference in clutch size between solitary and social full brood nests (Fig. 4; $t_{99,\ 6} = 2.45$, $P = 0.87$). Complete brood mortality was not observed in social colonies (0/6), but was found in 7/99 (7%) of solitary full brood nests, but these proportions were not significantly different (Fisher's exact test, $P = 0.5114$). However, the number of social full-brood nests here is

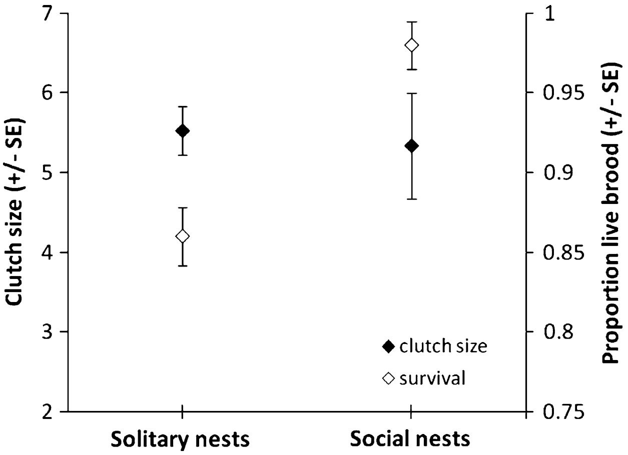

Fig. 4 Mean brood production and proportion of live brood in social and solitary full brood nests of *Ceratina australensis*. Social nests producing equal number of offspring as solitary nests. Solitary nests have fewer brood surviving to adulthood than social nests

small ($N = 6$) and it seems likely that some of our single-female full brood nests had initially started as social nests but where one nestmate had died prior to sampling. Such colonies are not detectable in our analyses, but it seems very unlikely that females suffer zero mortality between the start and finish of brood rearing. When analyses were based on all nests with brood (i.e. active and full brood nests), there was a significant difference in the proportion of live brood between solitary and social reproductive colonies (Fig 4; $\chi^2 = 6.74$, $P = 0.0094$). For these nests, mean per-nest brood mortality was 14% for solitary females and 2% for social nests.

Discussion

Our study found a low level of social nesting in *Ceratina australensis*, with only about 14% of the 262 colonies with active or full brood containing more than one adult female. This contrasts with some Asian species where rates of multi-female nesting were as high as 25% (Sakagami and Maeta, 1987; Rehan et al., 2009), and also differs from some Holarctic studies where females have never been found to nest socially during brood rearing (Malyshev, 1913; Kislow, 1976; Rehan and Richards, 2010). However, we note that our estimate of 14% is likely to be an underestimate, given that any colonies in our samples that began as social nests but where one female died prior to sampling would have been counted as a solitary nest.

In the following discussion we compare our results to other studies to consider life-history traits in ceratinines that may facilitate or constrain multi-female nesting during brood rearing. We then discuss reproductive differentiation and the nature of social colonies in *Ceratina* and conclude by asking whether low levels of sociality could represent a transitional stage to more frequent colony formation in the ceratinines.

Maternal behaviour and social preadaptations

The transition from solitary to eusocial life requires behavioural precursors from which overlapping generations, cooperative brood care and reproductive division of labour evolve. Such preadaptations include prolonged maternal care, maternal longevity and mutual tolerance (Wilson, 1971; Lin and Michener, 1972; Michener, 1985). Mothers of all studied *Ceratina* species demonstrate prolonged parental care and guard their brood throughout development (Kislow, 1976; Sakagami and Maeta, 1977; Rehan et al., 2009). All studied ceratinines also exhibit high frequencies of maternal survival and cohabitation with mature brood (Rau, 1928; Sakagami and Maeta, 1977; Johnson, 1988; Rehan et al., 2009; Rehan and Richards, 2010). In this study *C. australensis* adult females were found in 94% of nests with immature brood indicating nest loyalty and longevity in this species as well, both requisites for social cohabitation.

Maternal longevity is thought to influence brood survival as mothers protect their brood by acting as guards at the nest entrance (Kislow, 1976; Sakagami and Maeta, 1977). In this study we occasionally observed females inspecting brood cells. This behaviour is recurrent in ceratinines (Kislow, 1976; Sakagami and Maeta, 1977; Rehan et al., 2009, Rehan and Richards, 2010). Further interaction with brood is indicated by the relatively high frequency (47%) of mother–offspring cohabitation in mature brood nests. This subsocial interaction provides an early opportunity for contact and communication between mothers and offspring. This is in contrast to solitary bees that provision and seal brood cells and have no further contact with their developing offspring.

Female dispersal and social nesting

Dispersal prior to brood rearing has a very strong potential to limit social nesting since it breaks up kin groups. In the allodapines, cofounding of new nests by relatives has evolved only once, in the genus *Exoneura* (Schwarz et al., 2007). In all other species new nests are solitary founded and in most of these species the modal colony size is one (Schwarz et al., 2007). In our study only one of the 36 social *Ceratina australensis* colonies was in a new nest, suggesting that female dispersal is likely to constrain social nesting. Cofounding in natural populations of other *Ceratina* species is also very rare. *Ceratina australensis* overwinters in both newly founded and reused stems and the only other ceratinine reported to also disperse and found new nests in autumn is *C. (Ceratinidia) flavipes* (Kidokoro et al., 2003, 2006). In both these species, autumnal dispersal should therefore lower the potential for social nesting in spring, and *C. flavipes* only rarely (0.1% of nests collected) forms social colonies in the wild (Sakagami and Maeta, 1987). Conversely, *C. japonica* (a sympatric sister species of *C. flavipes*) does not disperse prior to overwintering and frequently forms social colonies in reused nests (63/203 or 31%), but rarely in newly founded nests (3/230 or 1.3%) during the spring brood rearing season (Sakagami and Maeta, 1987). Nest reuse is associated with social nesting of *C. (Ceratinidia) okinawana* as 57/276 or 14% of reused nests and only 1/133 or <1% of newly founded nests contained a multi-female association (Sakagami and Maeta, 1989). Likewise, in *C. (Ceratina) megastigmata* 4/5 multi-female colonies were found in reused nests (Katayama and Maeta, 1979). *Ceratina (Zadontomerus) calcarata* is another well-studied ceratinine that has never been observed forming social colonies and does not reuse nesting substrate (Kislow, 1976; Johnson, 1988; Rehan and Richards, 2010). These data suggest that social nests predominantly arise when females stay in a natal nest rather than joining a new nest.

Reproductive differentiation in social colonies

Behavioural differentiation among nestmates is pivotal to eusociality and a division of labour has been found in several bees thought to be incipiently social (Sakagami and Maeta, 1987; Wcislo, 1997; Jeanson et al., 2005). Social colonies of *C. australensis* contain only two females, and our data indicate that one female takes on both foraging and reproductive behaviour, while the second female has reduced ovarian development and wing wear suggesting neither reproduction nor foraging activity. This suggests that the reproductive female will only tolerate the presence of a nestmate if that nestmate is non-reproductive, but the non-reproductive female does not seem to take on any foraging duties. We therefore need to ask why a non-reproductive female is tolerated, and why that female should forego reproduction to remain as a non-reproductive, non-foraging nestmate. The social primary may tolerate the secondary female at the natal nest without contributing foraging effort, as the mere presence of the secondary might contribute to the colony by guarding brood while the primary reproductive is away from the nest. In addition, the social secondary may be a hopeful reproductive waiting to inherit the nest site from the social primary. This situation arises in social nests of some *Xylocopa* species (Hogendoorn and Velthuis, 1993, 1995; Steen, 2000), in which the dominant female is both the primary forager and the primary reproductive while the secondary female remains at the nest acting as a guard waiting for nest inheritance and supersedure. Other examples of auxiliary females remaining at the nest are found in some allodapine species where females remain at the nest in wait of future reproduction (reviewed in Tierney and Schwarz, 2009).

Body size is often a strong predictor of dominance in bee species without morphological castes (Batra, 1966; Michener, 1974; Packer, 1986; Hogendoorn and Velthuis, 1999). The association between reproductive differentiation and size difference is well documented in social nests of three Japanese species *Ceratina* (*Ceratinidia*) *japonica*, *C.* (*Ceratinidia*) *flavipes* and *C.* (*Ceratinidia*) *okinawana* (Sakagami and Maeta, 1984, 1987, 1989). Greater head width differences between females were associated with greater reproductive skew in these three species. In eusocial and semisocial colonies of these species the larger female took on guarding and primary reproduction while the smaller female took on a foraging non-reproductive role. When size difference was slight reproductive skew was incomplete and quasisocial nests, in which both females are reproductive, were most common. In *C. australensis* size-based reproductive dominance was not apparent. Size variation between females did not predict reproductive status as equal proportions of first and second body size-ranked females were reproductive.

Age is an additional predictor of reproductive differentiation among nestmates (Hogendoorn and Velthuis, 1999). Eusocial colonies require overlapping generations, usually in which the mother is dominant to her daughters. Conversely, reproductive dominance in semisocial associations may be attributable to a few days, if not hours, difference in eclosion among sisters (Schwarz and O'Keefe, 1991). In the absence of prolonged nest observations it was difficult to assess the age of bees from nest collections in our study as age estimates from wing wear scores are confounded with foraging effort. Social primaries were worn and secondaries were not. Therefore, whether nests contain semisocial sisters or eusocial mother–daughter associates remains unknown. Future study including observation of nests and/or genetic data should elucidate the age differentiation and status of each female in social colonies.

Brood productivity and social benefits

Two benefits of cooperative nesting have been identified for allodapine bees: (i) increases in per capita brood production, and (ii) prevention of total brood failure (Schwarz et al., 2007). In our study, social colonies were no more fecund than single foundress nests suggesting that the additional female did not contribute to brood rearing. In general, social secondaries had weakly developed ovaries and were not active foragers as their wings were unworn. Despite the absence of foraging behaviour by social secondaries, their presence could possibly contribute towards nest defence, either actively by blocking the nest entrance or passively by mere presence. We found no statistically significant increase in total brood size of social compared to solitary nests, and so per capita brood benefits are clearly not present in *C. australensis*. Although we found higher rates of total brood loss in solitary nests, this difference from social nests was not statistically significant. Overall, brood mortality was limited in this species. Our results therefore raise two important questions regarding sociality in *Ceratina*: (i) why do we not see the benefits of social nesting that are evident in most allodapines; and (ii) given the lack of apparent benefits in *C. australensis*, why do we see the low level of social nesting at all, given that secondaries are seemingly nonreproductive? Understanding these two issues is critical to discern why the preconditions for sociality can evolve, but not then facilitate the evolution of eusociality.

Given the lack of apparent benefits to group living it is a wonder why social colonies remain in this species. The sister tribe Allodapini provides many examples of life history and ecological traits that seem to select for group living. The combination of progressive provisioning and the omission of brood cell septa leave immatures vulnerable to starvation in the absence of continuous care as well as exposure to predation and parasitism (Schwarz et al., 2007; Zammit et al., 2008). Sociality in the allodapines therefore seems to provide a selective advantage over solitary life, concordant with their ubiquitous sociality with no reversions to purely solitary life (Chenoweth et al., 2007). Conversely, sociality in the ceratinines may not be so advantageous given their mass provisioning and construction of brood cells (Michener, 1974) requiring shorter durations of parental care and providing at least partial protection from predators and parasites.

It is thought that nest sharing evolved in bees and wasps because of the benefit of having more than one female available to defend the nest (Lin and Michener, 1972; Michener,1974). Most species of sphecid wasps are solitary, but one species, *Cerceris antipodes,* forms multiple female colonies which experience lower parasitism rates than solitary conspecifics (McCorquodale, 1989). Likewise, in the sweat bee, *Megalopta genalis,* multi-female nests experience less brood parasitism (Smith et al., 2003) and higher brood survival rates (Smith et al., 2007) than solitary nests from the same population. We found a slight decrease in brood loss between solitary and social nests and the observation of total brood loss in solitary colonies suggests a selective advantage for social colonies during periods of extreme parasitism pressure.

Taken together, nearly all social nests result from nest reuse and it seems likely that these nestmates are related. The near absence of newly founded social nests in *C. australensis* and other socially polymorphic ceratinines suggests that sharing a nest results from remaining at the nest rather than finding or founding a new nest. This suggests that kinship is important for sociality and that indirect fitness benefits are important for sharing a nest. In addition, we found evidence that sharing a nest lowers the rates of brood mortality, so that may be one source of indirect fitness, but there was no increase in per capita brood production. However, we also found that rates of brood loss in solitary nests were about 14%, but close to 0% for social nests. Because clutch sizes are the same for social and solitary nests, the benefits for the social secondary can at most be 0.14. Such a small value should strongly curtail altruism. This might help explain the rarity of social nesting in this species, but it still requires that costs for a social secondary must also be very small. This could be the case if social secondaries merely delay the onset of their brood rearing, and this does not lower the potential number of brood they can rear. The remarkable longevity of ceratinines supports the feasibility of delaying reproduction for a few months with negligible costs for social secondaries.

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