



Fitness consequences of ecological constraints and implications for the evolution of sociality in an incipiently social bee

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Ecological constraints such as resource limitation, unfavourable weather conditions, and parasite pressure have long been considered some of the most important selective pressures for the evolution of sociality. In the present study, we assess the fitness consequences of these three ecological factors on reproductive success of solitary nests and social colonies in the socially polymorphic small carpenter bee, *Ceratina australensis*, based on 982 nests collected over four reproductive periods. Nest site limitation was predicted to decrease opportunities for independent nest initiation and increase the frequency of social nesting. Nest sites were not limiting in this species and the frequency of social nesting was consistent across the four brood-rearing periods studied. Unfavourable weather was predicted to lower the frequency of female dispersal from their natal nests and to limit the brood-rearing season; this would increase the frequency and fitness of social colonies. Daily temperature and precipitation accumulation varied between seasons but were not correlated with reproductive success in this bee. Increased parasite pressure is predicted to increase the frequency and fitness of social colonies because solitary bees must leave the nest unattended during foraging bouts and are less able to defend the nest against parasites. Severe parasitism by a chalcid wasp (*Eurytoma* sp.) resulted in low reproductive success and total nest failure in solitary nests. Social colonies had higher reproductive success and were never extirpated by parasites. The high frequency of solitary nests suggests that this is the optimal strategy. However, social colonies have a selective advantage over solitary nesting females during periods of extreme parasite pressure, and we suggest that social nesting represents a form of bet-hedging against unpredictable fluctuations in parasite number. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, 103, 57–67.

ADDITIONAL KEYWORDS: parasite pressure – resource limitation – small carpenter – polymorphism – temporal variation.

INTRODUCTION

Environmental conditions have the potential to greatly influence the survival and fecundity of individuals, and their importance has been stressed for the evolutionary origins and maintenance of social behaviour in cooperatively breeding vertebrates (Woolfenden & Fitzpatrick, 1978; Emlen, 1991) and invertebrates (Lin & Michener, 1972; Evans, 1977; Strassmann & Queller, 1989; Wcislo, 1997). A growing

number of ecological studies has linked group living to constraints in species' biotic and abiotic environments and has found that resource limitation, climate and predation pressure can all play roles in selection for social behaviour. Although the importance of ecological factors has been emphasized for the evolution of social groups, there are few empirical studies tracking the selective pressure imposed by ecological constraints on both solitary individuals and social group fitness in sympatry.

First, depending on species and environment, resources can vary in abundance and ease of acquisition. The basic necessary resources are breeding

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sites and food, and competition for scarce resources may promote cooperation and group living (Alexander, Noonan & Crespi, 1991). In insects, cooperative breeding always involves multiple adults raising brood in a central nest (Crespi, 1994). When nests are difficult to construct or hard to find, then they may become a limiting resource that can be reused from one season to the next. Remaining at the natal nest to inherit such a valuable resource may be a better option than dispersing from the natal nest if chances of independent nest founding are low (Hogendoorn & Leys, 1993; Schwarz *et al.*, 2005; but see Bull & Schwarz, 1996).

Second, natural enemies are important agents of selection in the evolution of group living (Lin, 1964; Michener, 1985; Uetz & Hieber, 1997; Beauchamp, 2004). Nesting independently requires a single individual to obtain all brood provisions and therefore there are times when the nest is left unguarded. Guards at the nest provide protection against attacks on immatures in many social insects (Wcislo, West-Eberhard & Eberhard, 1988; McCorquodale, 1989; Sakagami, Gobbi & Zucchi, 1990; Matthews, 1991; Garofalo *et al.*, 1992) and the experimental removal of guards from social colonies leads to lower brood survival in bees (Smith, Wcislo & O'Donnell, 2003, 2007; Zammit, Hogendoorn & Schwarz, 2008), spider mites (Mori & Saito, 2005), and wasps (London & Jeanne, 2003).

Third, abiotic factors such as geographic location and local climate are known to have marked effects on life-history evolution studies. The effects of variation in climate on social behaviour in bees provide several testable hypotheses. Studies on facultatively social bees, such as those in which females are totipotent (capable of both solitary and social reproduction), have revealed that some sweat bees are social and produce two broods per year in areas with warmer temperatures and longer breeding seasons but are solitary in areas with cooler temperatures and shorter breeding seasons (Sakagami & Munakata, 1972; Packer, 1990; Eickwort *et al.*, 1996; Mueller, 1996; Hogendoorn & Leys, 1997; Soucy, 2002; Cronin & Hirata, 2003; Brady *et al.*, 2006; Weissel *et al.*, 2006).

The effect of variation in local weather conditions on social behaviour can be as marked as the effect of climate variation on a geographic scale (Sakagami & Hayashida, 1968; Packer, 1990; Hogendoorn & Velthuis, 1993; Yanega, 1993; Hirata & Higashi, 2008). For example, long-term studies of the obligately social sweat bee, *Halictus ligatus* (Richards & Packer, 1995), revealed that annual fluctuations in weather conditions influenced rates of brood survival and forms of social organization. Cold, rainy weather reduced the duration of time available for brood rearing, leading to smaller clutch sizes, and also

resulted in nest flooding, which led to brood rot resulting in high nest failure and low brood survival rates. Atypically warm weather resulted in an early onset of brood production, larger clutch sizes and, in turn, higher rates of worker oviposition (Richards, Packer & Seger, 1995) because worker numbers and pollen collection exceeded the queen's egg-laying abilities.

To our knowledge, no studies have contrasted a socially polymorphic species, with both solitary and social nests in the same population, over a series of brood-rearing periods to investigate how these sources of ecological variation might select for variation in social behaviour. The role of fluctuating environmental conditions has long been considered important for social insects and vertebrates but direct tests have been few (Strassmann & Queller, 1989; Emlen, 1991; Wcislo, 1997; Purcell, 2010).

Elucidating the environmental conditions that favour either solitary or social nesting strategies requires studying species in which both strategies occur in sympatry, so that the fitness consequences of each nesting strategy can be assessed over a series of brood-rearing periods. The Australian small carpenter bee, *Ceratina australensis*, is socially polymorphic (Michener, 1962; Rehan, Richards & Schwarz, 2010), with both solitary and social nests in the same population; thus, seasonal and social variation can be compared to examine fitness consequences of solitary and social reproductive strategies. In solitary nests, females forage and reproduce independently. In social colonies, a primary female behaves much like a solitary female, taking on foraging and reproductive duties, whereas a secondary female remains at the nest as a passive guard and delays reproduction until the next season (Rehan *et al.*, 2010). Females that disperse after eclosion to initiate new nests do so solitarily; however, females that reuse their natal nest may form social colonies. Adult females of this species often survive long enough to be reproductive in two consecutive brood-rearing seasons, either spring then summer, or summer then spring (Rehan *et al.*, 2010). *Ceratina* mothers mass provision brood in a single linear burrow and, when oviposition is complete, mothers remain with their nests until the brood reach adulthood (Sakagami & Maeta, 1977). This nest loyalty ensures that the contents of complete nests are an appropriate measure of reproductive success because maternal investment and reproductive effort is constrained to a single stem (Rehan & Richards, 2010).

The present study aimed to test predictions of temporal variation in three ecological factors (i.e. nest substrate availability, parasitism rates, and local weather) as influences on the expression of sociality and the fitness consequences for solitary and social

colonies of *C. australensis*. First, nest site limitation should decrease opportunities for females to found nests independently and increase the frequency of social nesting; an increase in nest site availability should decrease the frequency of social colony formation. Second, because solitary bees must leave the nest unattended during foraging bouts and are less able to defend the nest against parasites, we predict increased parasite pressure should increase the fitness and frequency of social colonies. Third, warm dry conditions in the brood-rearing season should promote prolonged brood-rearing periods and larger clutch sizes. Warmer weather is also expected to accelerate brood maturation; this in turn could favour higher rates of female dispersal and reduce the frequency and fitness of cooperative nesting. On the other hand, cool wet weather is predicted to lower the frequency of female dispersal and limit the brood-rearing season, which would increase the fitness and frequency of social colonies.

MATERIAL AND METHODS

In total, 982 *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 a.s.l.). Four collections during brood-rearing periods (N = number of nests) were undertaken over a period of 32 months in spring (first week of December) 2007 (N = 145) and 2008 (N = 165), and summer (first week of February) 2009 (N = 241) and 2010 (N = 289).

Nests were collected before 07.00 h to ensure that bees had not commenced flight activity for the day and all occupants would be present. All visible dead, broken fennel twigs with a round hole resembling a bee nest entrance were collected. Twigs were opened by splitting them lengthwise and, if they contained nests, the contents were recorded, including the number of brood cells, brood cell contents, developmental stages of brood, and numbers and locations of adult bees and parasites. Parasites were identified as a single species of chalcid wasp (*Eurytoma* sp.) by Dr John Huber at the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC) and voucher specimens are retained at the CNC.

Nests were categorized based on contents and overall appearance (Daly, 1966; Rehan, Richards & Schwarz, 2009). 'New' nests had clean walls devoid of pollen stains and faecal pellets, whereas 'reused' nests had darkened walls with pollen and/or faecal stains from previous provisioning and brood rearing in that twig. Complete or 'full brood' nests were those in which the cell closest to the nest entrance contains a larva or pupa, suggesting that the mother had

finished laying eggs. Full brood nests were collected at the end of the spring brood-rearing season (December) and at the end of the summer rearing period (February). For some analyses, we also included 'active brood nests' that contained pollen masses with eggs or small larvae, and which were deemed not to represent complete broods. 'Clutch size' is the total number of brood cells provisioned in a full brood nest. 'Live brood' is the total number of brood surviving to adulthood in a full brood nest. The proportions of eggs, larvae, and pupae in active and full brood nests were evaluated to compare rates of brood maturation among seasons. Samples with higher proportions of pupae would indicate faster rates of brood development, earlier onsets of brood provisioning, or both.

To assess potential nesting substrate limitation in this population, we increased nest site availability by cutting the tips off a patch of 186 fennel stems approximately 10 m away from an unaltered patch with existing bee nests. All stems in the altered patch were trimmed with pruning shears to expose bare pith, required for *Ceratina* to nest in these stems. This altered patch was marked with flagging tape in spring 2008 and surveyed for occupancy in summer 2009. If increasing the nest site availability leads to more frequent occupancy than in unaltered fennel patches, this would suggest that availability of dead broken stems may be limiting in the wild.

Climate data were obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au>) records for the weather station in the town of Warwick. *Ceratina australensis* are not active during winter months (Michener, 1962) when daily maximum temperatures fall below 25 °C, and thus we assumed that temperatures of at least 25 °C are required for bees to forage. *Ceratina australensis* does not forage when it is raining. Foraging days were defined as days above 25 °C with no rainfall. To estimate the duration of suitable weather for bee activity each season, the total number of days above base 25 °C was calculated for the brood-rearing periods in spring (October to November) 2007 and 2008 and summer (December to January) 2009 and 2010. Because brood cell provisioning and brood development take less than 55 days (Rehan *et al.*, 2010), weather data were compared for 2 months before nest collections to examine weather experienced by the bees during nest provisioning.

STATISTICAL ANALYSIS

Where measures of reproductive success (clutch size, brood parasitism, and brood survival) could not be transformed to fit assumptions of parametric analyses (Conover & Iman, 1981), we used Kruskal–Wallis nonparametric analysis of variance, Mann–Whitney

U-tests and chi-square goodness of fit tests compare temporal variation in reproductive success using SPSS, version 16.0 (SPSS Inc.).

RESULTS

WEATHER VARIATION AMONG BROOD-REARING PERIODS

There was considerable variation in temperature (Fig. 1A) and precipitation (Fig. 1B) accumulation among the four brood-rearing periods sampled between 2007 and 2010. The 2007, 2008, and 2009 brood-rearing periods were cool, whereas 2010 was average compared to the 30-year mean for each

season (Fig. 1A). The total precipitation accumulation (Fig. 1B) varied among periods; 2007, 2008, and 2009 were average and 2010 was dry compared to the other three periods. Combining temperature and precipitation accumulation for each brood-rearing period (Fig. 2), the spring 2007 and 2008 brood-rearing periods had ten fewer foraging days than the summer 2009 and 2010 periods. This indicates prolonged foraging opportunities in summer compared to spring brood-rearing seasons.

NEST SITE AVAILABILITY

To examine occupation rates in natural and enhanced patches for this species, all dead broken fennel twigs

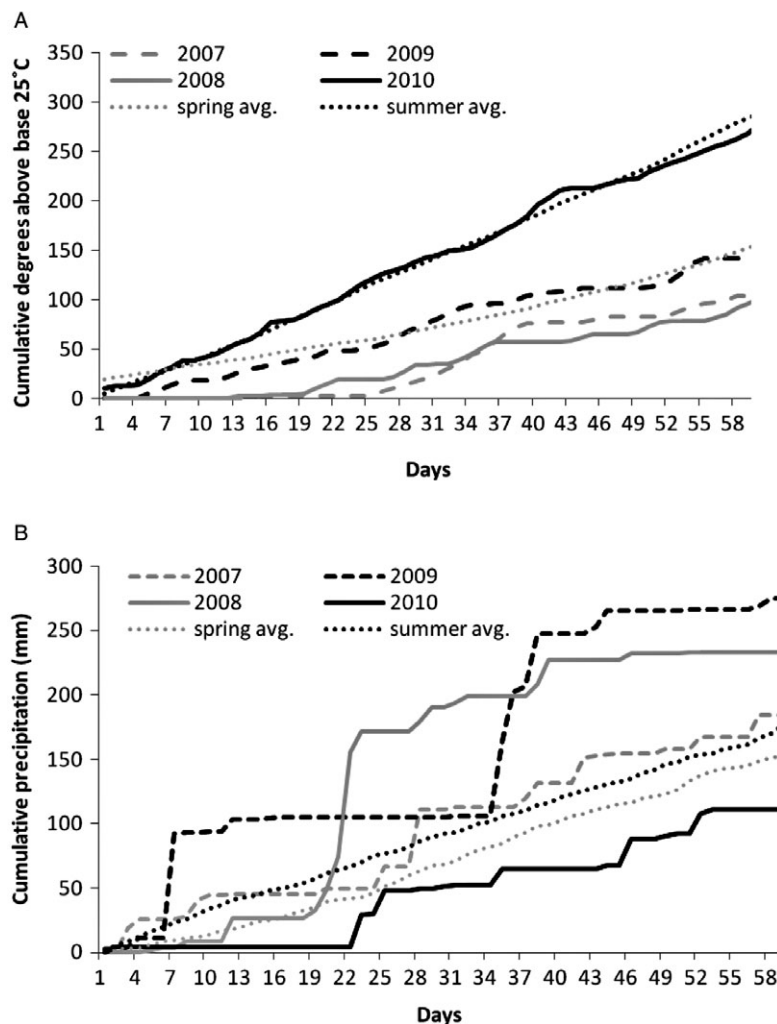


Figure 1. Weather data from Warwick, Queensland. Day 1 began on October 1 for spring (grey lines) and December 1 for summer (black lines) brood-rearing seasons. A, variation in average summer temperatures as represented by cumulative degree-days above base 25 °C during each brood-rearing period. Summer 2010 was average compared to the 30-year mean and spring 2007, spring 2008, and summer 2009 experienced cooler temperatures. B, variation in the amount of rainfall among reproductive seasons. The summer of 2010 was dry relative to the 30-year average and summer of 2009, spring 2007, and spring 2008 experienced greater rainfall.

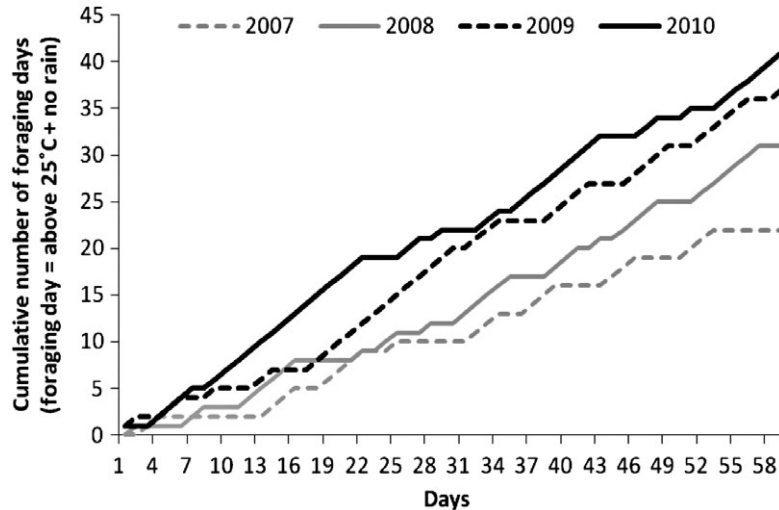


Figure 2. The number of foraging days per brood-rearing period. *Ceratina australensis* does not forage below 25 °C or when it is raining. The springs of 2007 and 2008 both had fewer foraging days than the summers of 2009 and 2010.

with a round hole resembling a putative bee nest were collected. From a total of 5332 twigs collected between 2007 and 2010, 982 (18%) contained *C. australensis*, 112 (2%) housed other insects, and 4238 (80%) were unoccupied. There was no significant difference in the proportions of unoccupied stems among collections ($\chi^2 = 4.339$, d.f. = 3, $P = 0.227$).

An ancillary patch of 186 dead fennel stems was cut back to expose bare pith and increase nest substrate availability in spring 2008. The next summer of 2009 (i.e. 2 months later), these stems were surveyed and 13 (7%) were occupied by *C. australensis*, two (1%) were occupied by other insects, and 171 (92%) remained unoccupied. There was no significant difference in the proportion of unoccupied stems between natural (991/1111) and artificially pruned (171/186) stems collected in summer 2009 (Fisher's exact test, $P = 0.317$). Both passive collections of unaltered patches and artificially increasing nest substrate availability revealed that occupied stems were used predominantly by *C. australensis*, whereas other insects were uncommon, and most stems remain unoccupied. The abundance of unoccupied stems suggests that nesting substrate is not limited.

VARIATION IN BROOD DEVELOPMENT

The relative ages of brood from all active and full brood nests collected suggest differences in the timing of nest initiation, in rates of brood development among seasons, or both. In spring 2007 (the first week of December), 19 active and full brood nests were collected, in which 3% (2/74) of immature brood were eggs, 42% (31/74) were larvae, and 55% (41/74) were pupae. Conversely, in spring 2008 (also collected

in the first week of December), 35 active and full brood nests contained no eggs, 31% (26/84) of brood were larvae, and 69% (58/84) were pupae. This suggests a slight but nonsignificant delay in brood development in the spring of 2007 compared to spring 2008 ($\chi^2 = 4.744$, d.f. = 3, $P = 0.09$). In summer 2009 (first week of February), from a total of 108 active and full brood nests, 24% (61/258) of immature brood were eggs, 29% (74/258) were larvae, and 48% (123/258) were pupae. In summer 2010 (also the first week of February), 216 active and full brood nests were collected, in which 13% (113/870) of immature brood were eggs, 33% (287/870) were larvae, and 54% (470/870) were pupae. Brood development was significantly delayed in the cool summer of 2009 compared to the average summer of 2010 ($\chi^2 = 17.33$, d.f. = 3, $P = 0.0001$).

VARIATION IN REPRODUCTIVE SUCCESS IN SOLITARY NESTS

The total number of full-brood social colonies in any collection period was too small to examine temporal variation in reproductive success; therefore, the data reported are for solitary nests only. The proportion of new versus reused solitary nests did not vary among brood-rearing periods ($\chi^2 = 12.00$, d.f. = 3, $P = 0.213$). There were no significant differences in clutch size (Kruskal–Wallis: $H = 0.18$, $P = 0.683$), number of brood parasitized (Kruskal–Wallis: $H = 0.12$, $P = 0.731$), or the number of live brood (Kruskal–Wallis: $H = 1.07$, $P = 0.303$) between new and reused nests.

We assessed temporal variation in brood production (clutch size), brood mortality (proportion of brood lost

to parasites), and reproductive success (number of live brood) across the four brood-rearing periods of spring 2007, spring 2008, summer 2009, and summer 2010. Clutch size did not vary significantly among brood-rearing periods (Kruskal–Wallis: $H = 1.625$, d.f. = 3, $P = 0.654$; Fig. 3A). Conversely, variation in the proportion of brood parasitized among brood-rearing periods was marked (Kruskal–Wallis: $H = 24.933$, d.f. = 3, $P < 0.001$; Fig. 3B). Nonparametric post-hoc tests for multiple comparisons between treatments (Siegel & Castellan, 1988) revealed that nests from 2008 experienced far less parasitism and 2009 significantly greater parasitism than the other years. Consequently, the number of live brood per nest also differed significantly among brood-rearing periods (Kruskal–Wallis: $H = 20.008$, d.f. = 3, $P < 0.001$; Fig. 3C). Post-hoc tests for multiple comparisons between treatments revealed that average brood survival was higher in 2008. It is noteworthy that the highest proportion of brood parasitism and low brood survival occurred during the cool to average season of summer 2009. By contrast, the lowest proportion of brood lost to parasitism and greatest number of live brood also occurred during a cool average season in spring 2008.

REPRODUCTIVE SUCCESS IN SOLITARY VERSUS SOCIAL NESTS

The overall frequency of social nesting was 12% (47/378 active and full brood nests). This frequency did not vary significantly among brood-rearing periods ($\chi^2 = 1.259$, d.f. = 3, $P = 0.74$; Fig. 4) and was independent of the frequency of nest reuse in the population ($\chi^2 = 0.017$, d.f. = 3, $P = 0.9842$). The number of full brood social nests was too small in any sample to examine temporal variation in reproductive success. Social colonies were found predominantly (46/47) in reused stems, such that the effects of nest reuse on reproductive success of social nests could not be assessed.

Social mothers were no more fecund than solitary mothers (Mann–Whitney: $U = 1.96$, $Z = 0.755$, $P = 0.451$), and variation in clutch size was no greater in solitary than social colonies (Levene's test: $F_{32,275} = 1.262$, $P = 0.262$; Table 1). The proportion of parasitized nests was not significantly different between solitary nests and social colonies ($\chi^2 = 0.29$, d.f. = 1, $P = 0.59$). The proportion of parasitized brood was not significantly lower in social colonies (Mann–Whitney: $U = 18.99$, $Z = 1.04$, $P = 0.298$). Parasites claimed 0–50% of brood cells per social colony but never caused complete mortality of the brood. Parasite severity was greater in solitary nests, resulting in total nest failure in 11/277 or 4% of solitary nests, although these proportions were not significantly dif-

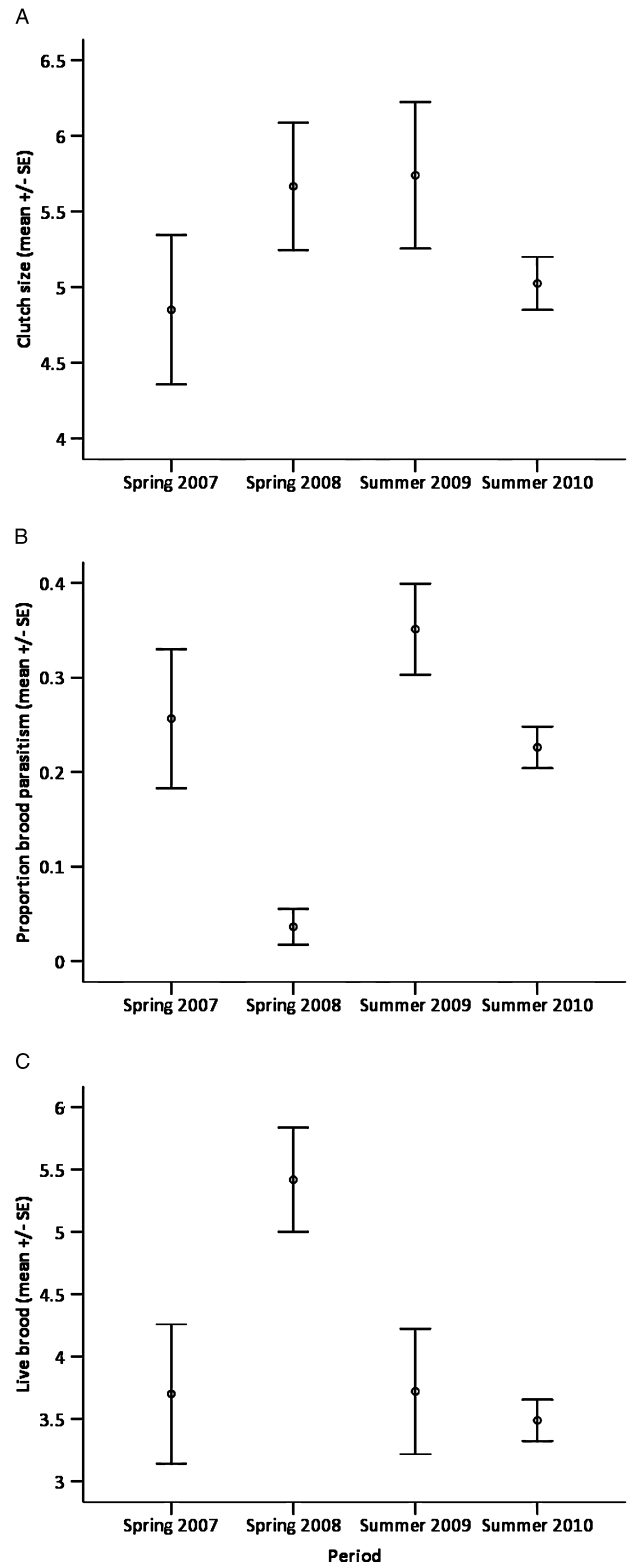


Figure 3. Temporal variation in reproductive success parameters in solitary full brood nests. A, clutch size; B, proportion of brood parasitized; C, number of brood surviving to adulthood.

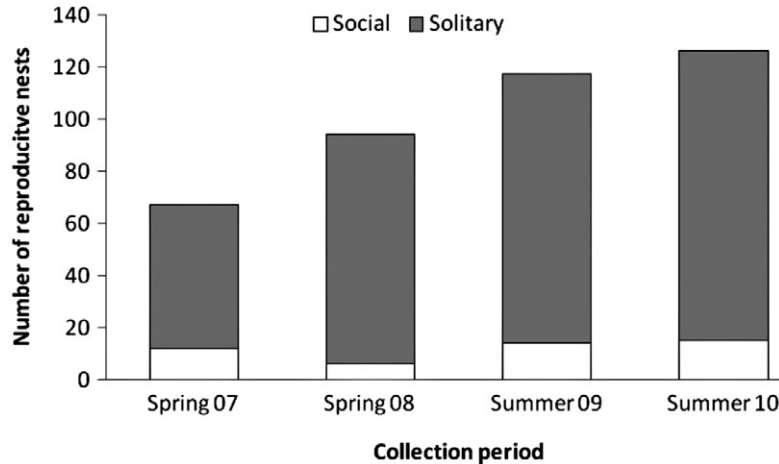


Figure 4. Frequency of social versus solitary colonies among four brood-rearing periods. There was no significant difference in the proportion of social colonies per collection. Overall, social colonies represent 12% of reproductive (active and full brood) colonies.

Table 1. Comparison of reproductive success measures in solitary versus social colonies of *Ceratina australensis* from Warwick, Queensland. Reproductive success values are averaged over full brood nests censused in spring 2007, spring 2008, summer 2009, and summer 2010

Reproductive success	Solitary (<i>N</i> = 277)	Social (<i>N</i> = 34)
Clutch size		
Range	1–15	2–10
Arithmetic mean ± SD	5.20 ± 2.66	5.32 ± 2.45
Number of parasitized brood		
Range	0–7	0–3
Arithmetic mean ± SD	1.20 ± 1.77	0.68 ± 1.01
Number of surviving brood		
Range	0–15	2–9
Arithmetic mean ± SD	3.77 ± 2.72	4.47 ± 2.02

ferent (Fisher's exact test, $P = 0.197$). When data from all samples were pooled, the number of live brood was significantly greater in social colonies (Mann–Whitney: $U = 15.90$, $Z = 1.904$, $P = 0.019$). Solitary nests had higher variance in the number of live brood than social nests (Levene's test: $F_{32,275} = 7.833$, $P = 0.005$; Table 1). Taken together, these data reveal a general pattern of more variable and lower mean reproductive success in solitary nests than in social colonies (Table 1).

DISCUSSION

We examined the fitness consequences of solitary and group living of *C. australensis* in response to three

ecological factors: local weather, nest site limitation, and parasite pressure. We found seasonal variation in local weather but, contrary to patterns in some other facultatively social bees, this was not associated with variation in the fitness or frequency of social colonies. Nest sites were not limiting and there was no variation in nest reuse patterns among brood-rearing periods. Conversely, parasitism did vary among brood-rearing periods and had a marked effect on reproductive success in this bee. Overall, the present study revealed that solitary and social colonies produce equivalent clutch sizes, although social colonies produce an overall higher number of live brood because of lower parasitism in multifemale nests.

Given the inherently variable nature of environmental factors over time, it is important to account for temporal variation and to estimate measures of fitness (e.g. brood survival) accordingly. Indeed, we observed a general pattern of more variable and lower mean reproductive success in solitary than in social colonies (Table 1). The results obtained indicate wide variation in reproductive success of solitary nests over the four brood-rearing periods that we sampled. At the same time, variation across a number of key nesting and brood-rearing traits was uneven, suggesting that environmental conditions had uneven impacts on several factors important for understanding life-history and social evolution. The predicted influences are addressed below, where we discuss variation in brood production and social behaviour.

ENVIRONMENTAL CONSTRAINTS ON DEVELOPMENT RATES AND BROOD PRODUCTION

Warmer temperatures cause faster development in insects (Pruess, 1983). Therefore, it is not unexpected

that there was a significant difference in rates of brood development among brood-rearing periods. Warmer and drier periods were associated with a higher proportion of pupae than larvae in brood-rearing nests. Advanced brood development could also indicate an earlier onset of brood provisioning in warmer weather as found in studies on sweat bees (Richards & Packer, 1995; Cronin & Hirata, 2003; Hirata & Higashi, 2008). Early onset and prolonged warm temperatures during brood-rearing periods hasten brood maturation allowing more time for females to initiate nests independently and promote the dispersal of adult females, thus reducing the frequency of multifemale nesting associations.

Clutch size did not vary among brood-rearing periods. This is significant given the marked variation in weather parameters and contrasts with some other bee studies in which warm dry conditions were correlated with increased clutch sizes (Packer *et al.*, 1989a; Packer, 1990; Richards & Packer, 1995; Cronin & Hirata, 2003), with increased brood production being generally attributed to prolonged foraging durations in warm dry conditions (Minckley *et al.*, 1994; Richards, 2004). In the present study, precipitation also had no observed effect on clutch size. Precipitation can have drastic effects on ground-nesting bees, leading to flooding, mould, and mortality of brood (Packer & Knerer, 1986; Packer *et al.*, 1989b; Heide, 1992; Packer, 1992; Richards & Packer, 1995; Fields, 1996). Twig-nesting bees such as *C. australensis* remain sheltered from flooding by their elevated nesting habitats, and apparently suffer no other ill effects because we did not observe any signs of brood rot.

An explanation for the lack of temporal clutch size variation in the present study may be that this species is not pollen limited; ceratinine females do not forage for the entire brood-rearing season but, instead, provision a set number of cells and then sit and protect their brood. Clutch sizes of *C. australensis* are reasonably small, with an average of five offspring per nest (range 1–15). Foraging observations on Japanese congeners indicate that females are capable of provisioning 1.6 brood cells in a single foraging day (Maeta, de la Sierra & Sakagami, 1997). If *C. australensis* provisions at approximately the same rate, then females would require as few as 3–10 foraging days to provision complete broods. This is in contrast to the 20–40 foraging days available per brood-rearing season (Fig. 2) and suggests that, in *C. australensis*, foraging time is not limited by weather. In addition, female carpenter bees lay very large eggs and lay at most a single egg per day (Iwata & Sakagami, 1966). Consequently, egg limitation may set an upper limit on clutch size rather than provisioning time or pollen availability (Minckley *et al.*, 1994; Rosenheim, 1996).

The lack of temporal clutch size variation is further supported by the fact that ceratinine mothers provide prolonged parental care after foraging to sit and protect their brood for the duration of development, inspect brood cells (Rehan *et al.*, 2009, 2010; Rehan & Richards, 2010), and feed offspring prior to dispersal (Sakagami & Maeta, 1977). The consistent clutch sizes found in *C. australensis* (present study) and congeners (Vickruck, Huber & Richards, 2010) may be attributable to the energetic requirements of such egg limitation and prolonged maternal care rather than pollen availability or weather variation (Neukirch, 1982; Schmid-Hempel, Kacelnik & Houston, 1985; Cartar, 1992).

THE EFFECT OF BROOD PARASITISM ON REPRODUCTIVE SUCCESS

By contrast to the lack of temporal variation in clutch sizes, we found significant variation in rates of brood parasitism among brood-rearing periods. *Eurytoma* sp. was the only parasite found in the present study. *Eurytoma* are known parasites of *Ceratina* (*Zadonotomerus*) species from the Nearctic (Bugbee, 1966; Daly, Stage & Brown, 1967; Vickruck *et al.*, 2010) and *Ceratina* (*Euceratina*) *callosa* in the western Palearctic (Grandi, 1961). The parasite is assumed to enter the stem at the entrance and lay its eggs in a series of consecutive cells (Daly *et al.*, 1967). The life history of this parasitoid species is unknown but appears to be synchronous with that of its host. Late-stage pupae of both the bee host and its parasite were collected in spring and summer broods, which suggests that the parasite, similar to its host, is bivoltine in southern Queensland.

There was a marked increase in parasite pressure and decreased brood survival during the cool summer of 2009. Bees forage less frequently but take longer foraging trips in cooler ambient temperatures (Minckley *et al.*, 1994; Rands & Whitney, 2008). A prolonged absence of the mother from the nest leaves the brood vulnerable to invasion by parasites and predators, even if the total time the bee is absent from the nest does not vary (Goodell, 2003). Given the similar rates of brood production under different weather conditions, variance in reproductive success of *C. australensis* may be attributable to changes in parasite pressure (Goodell, 2003; Lienhard *et al.*, 2010).

Parasite avoidance is a strong selective factor contributing to the maintenance of social nesting. Parasites can claim up to 90% of brood in solitary bees (Bohart, Stephens & Eppley, 1960) and some bee aggregations have been completely extirpated by parasites (Batra, 1966). Increased abundance of parasites in this population could favour group living in *C.*

australensis. The present study revealed a decreased brood mortality in social nests, suggesting a marked benefit to retaining a secondary female at the nest.

NEST SUBSTRATE LIMITATION AND SOCIAL NESTING

Rates of nest reuse did not vary significantly across the four brood-rearing periods examined; bees in newly-founded nests represented the majority (approximately two-thirds) of the population each year. Similarly, there was little variation in the relative frequency of social colonies, which are largely restricted to reused nests in this (this study; Rehan *et al.*, 2010) and other *Ceratina* species (Sakagami & Maeta, 1977, 1989; Rehan *et al.*, 2009). Low frequencies of nest reuse consistent across all brood-rearing periods may limit the extent to which social nesting can occur. Because dispersal occurs during the breeding period before reproduction (Rehan *et al.*, 2010), high rates of dispersal in one season should limit the ability of these bees to respond to increasing parasite pressures that might make social nesting advantageous in the next. If constraints such as parasitism that may give social nests an advantage are not predictable on the basis of recent or current conditions, then we may not expect much variation in rates of social nesting.

Social polymorphism in *C. australensis* may therefore result from bet-hedging by social nesting bees (Seger & Brockmann, 1987; Yanega, 1988; Frank & Slatkin, 1990). The high frequency of solitary nesting suggests that it is the optimal strategy when parasite pressure is low but social nesting is advantageous when parasite pressure is high. If high rates of parasite pressure are unpredictable in the previous season when dispersal occurs, then a polyphenism of solitary and social behaviour would be maintained over time (Cohen, 1966). When stochastic elements are introduced into fitness models, strategies that lead to higher average numbers of offspring need not necessarily increase in frequency over long periods of time (Gillespie, 1977). Rather, natural selection tends to favour both large mean fitness and small variance in fitness (Stearns, 2000; Orr, 2007). By minimizing variance in reproductive success between reproductive bouts, bet-hedging by social nesters results in lower reproductive success in some periods, although total nest failure will claim fewer social colonies of *C. australensis*. Therefore, the benefits of reduced variance in reproductive success reduce the cost of lower fitness in any given brood-rearing period.

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