The costs and benefits of sociality in a facultatively social bee

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The evolution of social behaviour from solitary antecedents has traditionally been attributed to inclusive fitness benefits. Direct fitness components account for individuals' lifetime reproductive success through the production of offspring. In contrast, indirect fitness components account for the transmission of genes via aiding relatives and may explain apparent altruism among some members of social groups. Hamilton's rule gives the conditions under which altruism may evolve, but measuring the parameters in Hamilton's rule has proved to be very difficult for most social species. Here we quantify direct and indirect fitness in a facultatively social bee, *Ceratina australensis*, capable of both solitary and social nesting. Social colonies of this species contain one reproductive (the primary) and one nonreproductive female (the secondary), and it is therefore straightforward to measure the lifetime fitness of each individual. In the absence of the primary, the secondary female is fully capable of reproduction and produces equivalent numbers of offspring as solitary females. Per capita brood production was lower in social colonies than solitary nests. We found that inclusive fitness arguments do not explain social nesting in this bee. Moreover, social nesting cannot be attributed to subfertility or manipulation. The frequency of natal nest reuse is highly correlated with the frequency of social nesting in this and other *Ceratina* species. In other words, social nesting might be influenced by dispersal patterns and latent genetic differences in any tendency for natal philopatry. We argue that for *C. australensis* and perhaps many species with simple forms of sociality, life history traits such as nest reuse and natal philopatry are key selective factors for the origin of group living. Future work on this and other *Ceratina* species will reveal genetic, life history and ecological correlates with transitions in social evolution and their potential causes.

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Social insects often dominate their ecological niches, yet, paradoxically, sociality has evolved relatively few times (Wilson, 1971). Hamilton (1964) proposed that since social groups typically consist of related individuals, an altruist could accrue indirect fitness by helping collateral relatives to reproduce. Inclusive fitness is the sum of an individual's direct fitness, via direct reproduction, and indirect fitness, through aiding relatives to reproduce. Inclusive fitness has been defined as 'the effect of one individual's actions on everybody's numbers of offspring …weighted by the relatedness' (Grafen, 1984, page 67). According to Hamilton's rule, for the simplest pairwise comparisons, individuals could sacrifice reproduction and still pass on more genes when $r_k b > r_o c$, where r_k is the relatedness of the altruist to the recipient's offspring, b is the number of extra related offspring raised to maturity as a result of the altruist's actions, r_o is the relatedness of an individual to its own offspring, and c is the number of offspring that the altruist sacrifices by helping.

When comparing social to solitary modes of reproduction, the major question usually asked is why do helpers help? In other words, why would an individual forgo reproduction in order to aid the reproduction of others? This focal question has also been termed 'the paradox of altruism' and is vital to our understanding of the evolution of social life. The prominence of this focus, however, has resulted in neglect of the corollary question: why do individuals accept help? Ignoring this question suggests the tacit assumption that accepting help always leads to a net benefit, but there is evidence that group living can be costly and helpers may actually have detrimental effects on the fitness of those they help. For instance, in paper wasps there are diminishing per capita fitness returns in larger colony sizes, with declining ergonomic efficiency if there are more workers than there are tasks to be performed (Wenzel & Pickering, 1991). Halictid bee workers often reproduce selfishly, lowering the maximum potential fitness of queens (Richards, Packer, & Seger, 1995). In carpenter bees, solitary females

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sometimes experience higher fitness than dominant females with helpers (Hogendoorn & Velthuis, 1993; Stark, 1992). Therefore, it is also important to ask whether dominant individuals should accept help and whether they actually do benefit from having helpers at the nest.

One mechanism that potential altruists can use to direct their help towards rearing nondescendent kin is to become alloparents in their natal nest. This behaviour has the benefit of avoiding the costs and risks of dispersal, while taking advantage of reproductive opportunities at home. If the number of related offspring raised is high, then the inclusive fitness benefits accrued by remaining at the natal nest to cooperatively rear a relative's offspring could be greater than the cost of forgoing or failing reproduction. Likewise, if the number of offspring sacrificed by an altruist is low, the inclusive fitness of helping might be greater than that obtained by reproducing directly.

Despite the fact that inclusive fitness theory is widely accepted as the explanation for the evolution of sociality, empirical tests of inclusive fitness theory in social insect populations are few (e.g. Gadagkar, 2001; Leadbeater, Carruthers, Green, Rosser, & Field, 2011; Metcalf & Whitt, 1977; Richards, French, & Paxton, 2005; West-Eberhard, 1969). Previous attempts to evaluate inclusive fitness theory in social insects mostly involve obligately social species, where the question being asked is whether any particular individual should act as a selfish reproductive or a helpful subordinate, always within a highly derived social context. For example, some studies on obligately social paper wasps found that sociality is favoured because multiple (pleometrotic) foundresses have higher inclusive fitness than single (haplometrotic) foundresses (Gadagkar, 2001; Metcalf & Whitt, 1977; West-Eberhard, 1969), and others have found that there are delayed, direct fitness benefits to helping, because helpers often inherit nests and become dominant egg-layers (Leadbeater et al., 2011). Moreover, nest inheritance and delayed direct reproduction can be great enough to benefit even unrelated helpers (Leadbeater et al., 2011). A study on obligately social sweat bees also estimated r, b and c for queens and workers (Richards et al., 2005). This study suggested that helping behaviour benefits the queen but not workers in terms of inclusive fitness, suggesting that, in terms of inclusive fitness, social nesting can be advantageous to some individuals but not to others.

Previous studies offer important insights into the maintenance and elaboration of obligate social groups, in which all individuals form social associations, and help to explain reproductive decisions by individual females. However, they do not provide a genuine comparison of the adaptive significance of social versus solitary nesting strategies. To date, only one study on social insects has actually attempted to compare lifetime fitness for individuals breeding solitarily and in groups. Stark (1992) evaluated r, b and c in the carpenter bee, *Xylocopa sulcatipes*. This species is facultatively social, forming both solitary and two-female social colonies; the inclusive fitness of solitary nesters and helpers favoured the maintenance of both reproductive strategies depending on ecological conditions. Unfortunately, the fitness consequences for dominant females of having helpers in social nests were not addressed, and so this study provides no insight into why a dominant bee should accept a subordinate, especially given the risks of nest usurpation and oophagy by nestmates (Stark, 1992).

A basic problem in understanding the evolution of sociality is to empirically measure the inclusive fitness of alternative strategies to determine the conditions under which sociality would spread or be maintained in a population. Such measurements need to be carried out over as many generations as possible because short-term studies may not capture important stochastic variation in the parameters of Hamilton's rule. For example, predator or parasite pressure could favour social living, because of the benefits of nest

defence and antipredator vigilance (Lima, 1995; Smith, Wcislo, & O'Donnell, 2007; Zammit, Hogendoorn, & Schwarz, 2008), but may not be evident in periods when enemies are not common. Facultatively social species provide an ideal situation to study the selective advantages of solitary versus social reproduction, because females are totipotent and capable of breeding solitarily, as social reproductives or as social helpers. This means one can test the parameters of inclusive fitness models (r, b and c) for solitary and social nesters living in the same environment at the same time. However, it is also important that such evaluations are carried out over multiple reproductive periods, so that variation in selective pressures can be taken into account. Analyses in this vein are critical for proper evaluation of how Hamilton's rule and inclusive fitness apply to the initial stages of social evolution (Bourke, 2014).

The bee subfamily Xylocopinae has been widely used to examine insect social evolution (Schwarz, Richards, & Danforth, 2007) and comprises four tribes, Manueliini, Xylocopini, Ceratinini and Allodapini. Recent studies have shown that simple forms of sociality are ancestral for the Xylocopinae and have been present for about 100 million years (Rehan, Leys, & Schwarz, 2012). However, despite this very long-term history of social nesting, sociality involving strong forms of altruism (e.g. the presence of a true worker caste) are derived and restricted to the Allodapini. Studies on allodapines have reported high levels of relatedness within colonies, and have also reported high benefit/cost ratios associated with the presence of subordinate females (Schwarz et al., 2007). Studies on the Xylocopini have found a benefit to helpers at the nest through guarding (Hogendoorn & Leys, 1993; Stark, 1992; reviewed in Bourke, 2014). On the other hand, studies of Ceratinini have not provided firm numerical estimates of either relatedness or the effect of subordinates on colony productivity. Consequently, we do not know whether the lack of true worker castes in this tribe is due to low relatedness, low b/c ratios, or both.

Ceratina australensis (Xylocopinae: Ceratinini) is a facultatively social carpenter bee with both solitary nests (~87%) and social colonies (~13%) in the same populations (Rehan, Richards, & Schwarz, 2010). Social nests consist of only two individuals, and the frequency of solitary and social colonies does not appear to vary annually (Rehan, Schwarz, & Richards, 2011). Females that disperse after eclosion to initiate new nests do so solitarily; however, females that reuse their natal nest may form social colonies (Rehan et al., 2010). Adult females of this species often survive long enough to be reproductive in two consecutive brood-rearing seasons (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 reaches adulthood (Rehan & Richards, 2010a). This nest loyalty ensures that the contents of complete nests are an appropriate measure of reproductive success for females surviving any one reproductive episode because maternal investment and reproductive effort is constrained to a single stem (Rehan et al., 2010; Rehan & Richards, 2010a). Importantly, social colonies show high reproductive skew in which the primary female forages and lays eggs, while the secondary female guards but does not forage or lay eggs (Rehan et al., 2010). Unlike many other species, where sociality can be complex, the small colony size and simplicity of sociality in *C. australensis* make it much easier to measure r, b, and c.

Here we provide the first numerical estimates of relatedness for a ceratinine bee, based on direct genetic data rather than inferences about likely pedigrees (which can be misleading if there is multiple mating or undetected nest switching). Our data also allow us to estimate likely b/c ratios based on multiple years of observation with large sample sizes. Our study tests two related hypotheses. First, females should nest cooperatively when the per capita lifetime reproductive success of social nesting exceeds that of solitary

nesting. By contrast, females should assume a solitary lifestyle when lifetime reproductive success is greater for solitary nesting. Second, when nesting cooperatively, both primary (reproductive) and secondary (nonreproductive) females are expected to have greater fitness than solitary reproductives, because primaries receive help, which should allow them to reproduce at a higher rate, and secondaries should be able to compensate for their loss of direct fitness by increasing their inclusive fitness.

METHODS

Life History

Ceratina australensis is a stem-nesting, small carpenter bee endemic to Australia. Adult females are able to reproduce in two consecutive brood-rearing seasons (Rehan et al., 2010). New nests are founded by solitary females, and social colonies are formed when females remain together in their natal nest (Rehan et al., 2010). Social nests are occupied by only two adult females. The 'primary' female is both the forager and the reproductive, whereas the 'secondary' remains in the nest, neither foraging nor reproducing. However, if the primary female dies, the secondary female commences foraging and oviposition, thereby assuming the role of a solitary female. This means that a social secondary rarely or never contributes eggs to the first brood, but may contribute eggs to the second brood upon the death of the social primary. Since females accumulate wing wear as they forage, nest inheritance by a social secondary is evident when a nest contains an unworn adult female but advanced-stage brood (Rehan et al., 2010).

Nest Collections and Brood Production

Ceratina australensis nests were collected intact from dead broken stems of giant fennel (*Ferula communis*) in Warwick, Queensland, Australia. Nests were collected along rural road sides and not on privately owned or protected areas. Nests were collected at dawn and dusk to ensure that all adults would be present. Nests were collected by pruning each stem at the base of the stalk and nest entrances were sealed with masking tape. Nests were chilled on ice for transport back to the laboratory. Nest dissection involves splitting the stem longitudinally with a knife. At the time of nest dissection, total nest contents were recorded, including the number of adult females, the number of brood cells and the total number of parasitized brood. After nest dissection, adult bees were placed in individual plastic tubes and into a $-20\,°C$ freezer to be euthanized. A total of 840 nests were surveyed in four brood-rearing seasons: 2007 (145 nests), 2008 (165 nests), 2009 (241 nests) and 2010 (289 nests).

We determined clutch size by counting the total number of brood cells in each nest. Only full brood nests were used for fitness estimates for each brood (Rehan & Richards, 2010b). These 'full brood' nests are those in which the cell closest to the nest entrance contains a larva or pupa, suggesting that the mother had finished laying eggs (Rehan & Richards, 2010b). Offspring were raised in the laboratory and there was no significant difference in unparasitized brood mortality between solitary and social nests (Rehan et al., 2010). Offspring were monitored daily, and upon final eclosion, adult offspring were euthanized the same day by transferring them to a $-20\,°C$ freezer. Eighty seven per cent of all offspring mortality was due to parasitism by a chalcid wasp (*Eurytoma* sp.), and consequently offspring mortality rate is largely influenced by parasite pressure in the population (Rehan et al., 2011). Brood survival rate was determined by dividing the total number of brood that survived to adulthood by the clutch size of each brood (Rehan et al., 2010). Nests were collected and dissected each season. It was impossible to repeatedly survey the same nest in the field because of the destructive means by which nests were dissected. Instead, hundreds of colonies were collected and quantified at each time point to provide population estimates of each reproductive strategy. Direct fitness was defined as the total number of brood produced by females of each reproductive strategy that survived to adulthood.

Relatedness Estimates

Using allozyme electrophoresis, we genotyped 153 adult and callow bees from 46 nests (33 solitary and 13 social colonies) collected in the February 2009 sample. Bees used for allozyme analysis were killed by freezing at $-80\,°C$ in individual 1.5 ml microcentrifuge tubes and stored until assay. Details of allozyme markers employed are listed in Supplementary Table S1 (Richardson, Baverstock, & Adams, 1986).

We used Arlequin 2.001 (Schneider, Roessli, & Excoffier, 2000) to test for linkage disequilibrium among loci and Hardy–Weinberg equilibrium of each locus. These tests were based on a subsample of one randomly selected female per nest. Pairwise linkage disequilibrium values for all loci were ranked and the sequential Bonferroni correction (Hochberg, 1988) was applied to P values adjusting for multiple comparisons. The inbreeding coefficient was estimated using the computer program Relatedness 4.2 (Queller & Goodnight, 1989), which was also used to calculate relatedness estimates for mother–offspring and social female pairs. Relatedness 4.2 was also used to generate expected distributions of pairwise relatedness values for specific pedigree relationships, based on the observed frequencies of alleles in our study. For each pedigree simulation, 1000 pairwise values were generated. It is important to note that because only 11 loci were used for estimating relatedness, point estimates are imprecise and values less than zero may be due to stochasticity in genotype frequencies rather than negative assortment of individuals with respect to genetic similarity. Intracolony relatedness observed between social females and expected based on haplodiploid relatedness for putative two-female relationships was calculated for pairwise values using 11 loci and 13 colonies. These data were compared to simulated values based on the same number of alleles and allele frequencies as for the empirical data, but specific pedigree relationships. Estimates are reported as regression relatedness values and can range from positive to negative values. Zero relatedness represents the average relatedness of any two randomly drawn individuals from the sampled population as a whole (Bourke & Franks, 1995; Grafen, 1985). Negative relatedness indicates that two individuals are less related than any pair of individuals from the population, and positive relatedness indicates that relatedness between pairs is higher than average.

Statistical Analyses

Where measures of fitness (clutch size and brood survival) could not be transformed to fit assumptions of parametric analyses, we used Kruskal–Wallis nonparametric ANOVA, Mann–Whitney *U* tests and chi-square goodness-of-fit tests to compare difference in reproductive success using SPSS, version 16.0 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

Bees were euthanized in the most humane way possible. All work was conducted in accordance with regulations and guidelines established by the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes and the Flinders University
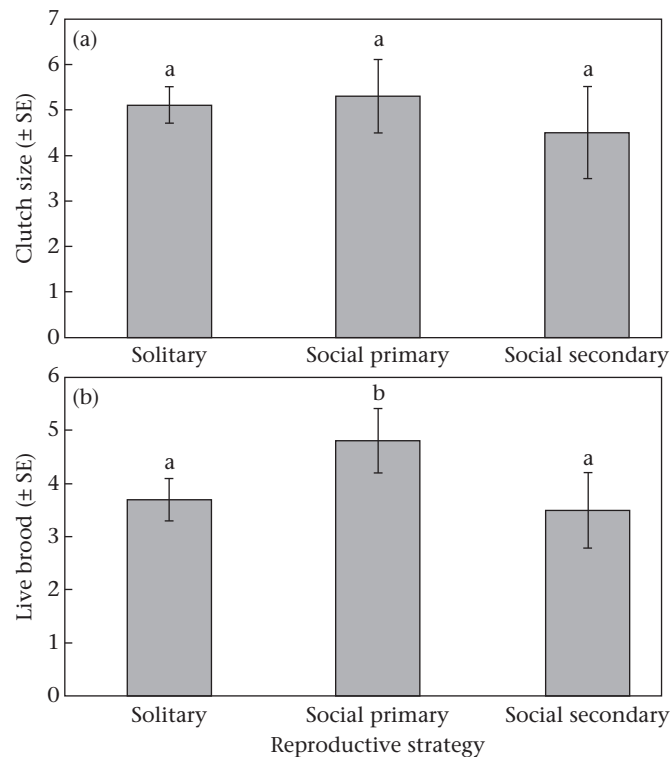
Animal Welfare Committee. No licences or permits were required for this research.

RESULTS

Brood Productivity

Solitary females produced similar numbers (mean ± SD) of offspring in first and second broods (first brood: 5.1 ± 2.7 offspring, $N = 95$; second brood: 5.1 ± 2.0 offspring, $N = 180$; Mann–Whitney U test: $Z = -1.096$, $P = 0.27$). Social primaries also produced similar clutch sizes in first and second broods (first brood: 5.3 ± 2.7 offspring, $N = 11$; second brood: 5.2 ± 3.0, $N = 21$; $Z = -1.36$, $P = 0.20$). Social secondaries inherited nests in 10/57 (17%) initially social colonies. When nests were reused by secondary (unworn) females for their first brood of reproduction, their mean clutch size was 4.5 ± 2.3 offspring ($N = 10$ nests). Since first and second brood clutch sizes were not different in social nests, there was no overall difference in clutch size among solitary, primary and secondary females (median = 5, interquartile range (IQR) = 3–7 offspring for all strategies; Kruskal–Wallis test: $\chi^2_2 = 1.26$, $P = 0.53$; Fig. 1a).

Solitary females produced similar numbers of offspring surviving to adulthood in their first and second broods (first brood: 3.7 ± 2.7 offspring, $N = 95$; second brood: 3.2 ± 2.4 offspring, $N = 180$; median = 3, IQR = 2–5; Mann–Whitney U test: $Z = -0.121$, $P = 0.90$). Likewise, social primaries produced similar numbers of offspring in each brood (first brood: 4.8 ± 2.9 offspring, $N = 11$; second brood: 3.7 ± 2.0 offspring, $N = 21$; median = 4, IQR = 2–5; $Z = -0.78$, $P = 0.58$). Social secondaries whose primary had died produced 3.5 ± 2.4 surviving offspring (median = 3, IQR = 2–5, $N = 10$). On average, primary females produced more offspring per clutch that survived to adulthood than either solitary or secondary females (Kruskal–Wallis test: $\chi^2_2 = 18.9$, $P < 0.0001$). Brood survival (84%) was significantly greater in social colonies when both primary and secondary female were present, than in solitary nests and those inherited by the social secondary (72%; Student–Newman–Keuls post hoc test: $P < 0.05$; Fig. 1b). Therefore, in subsequent analyses brood survival rates were considered separately for each reproductive strategy.
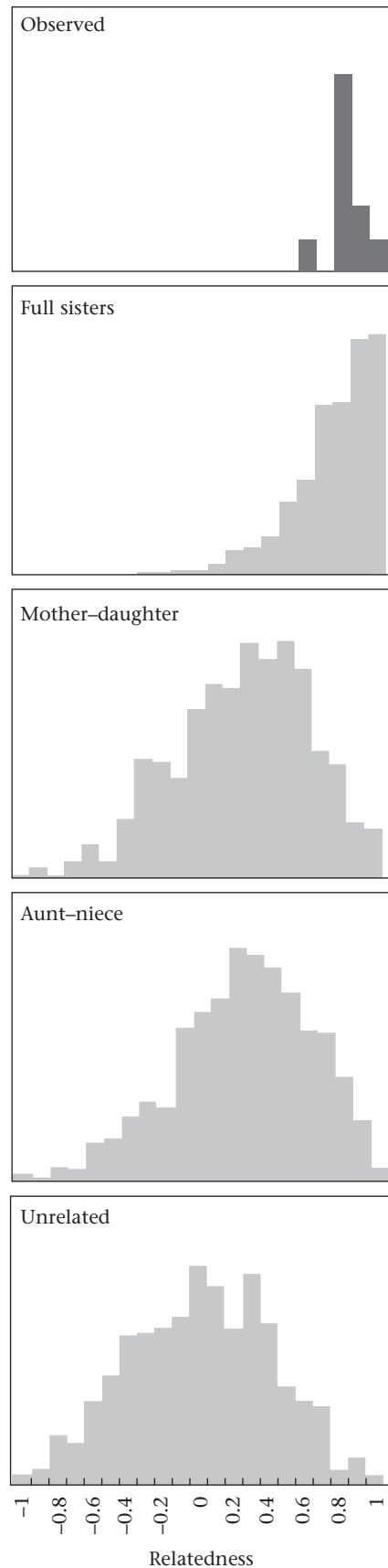
Relatedness Estimates

Eleven of the 47 putative allozyme loci successfully assayed (Table S1) were polymorphic and consistent with Mendelian inheritance at single loci. Chi-square tests revealed that the observed allele and genotype frequencies did not differ significantly from the expected allele and genotype frequencies under Hardy–Weinberg equilibrium for any locus ($P > 0.05$ for all comparisons). There was no evidence of linkage disequilibrium among the loci (10 000 permutations per pair of loci, Bonferroni corrected: $P > 0.05$). The inbreeding coefficient jackknifed over loci was not significantly different from zero ($F_{IT} = 0.009$, $P = 0.074$). Visual inspection of genotypes revealed that all colonies were monandrous and monogynous with no signs of multiple mating or 'alien' genotypes within colonies.

In Fig. 2 we have graphed the expected distributions of relatedness for four types of pedigree relationships between two females, namely full sister, mother–daughter, aunt–niece and unrelated females. The observed relatedness between female nestmates ($r = 0.79 ± 0.09$; Table 1) closely matched that expected for full sisters (0.75). The 95% confidence intervals were calculated to compare relatedness estimates with the expected regression relatedness (Table 1) for colonies comprising a singly mated female and her brood (Bourke & Franks, 1995). Relatedness estimates from the 11 polymorphic allozyme loci for cohabiting primary and secondary females were all well within the 95% confidence interval expected for a full sister (also termed semisocial) associations. As a result, the average relatedness of a secondary to a primary's offspring (r_k) ought to match the expected value of 0.375.

Direct Fitness of Solitary and Social Females

To calculate the direct fitness of each reproductive strategy, calculations were based on average brood production and observed brood survival rates. This method was employed because clutch size did not vary significantly between social primaries, social secondaries that inherited a nest and solitary nesting females, but there was a significant difference in brood survival among these reproductive strategies. Solitary females produced, on average, 10.4 offspring over their lifetime, 7.5 of which survived to adulthood. In social nests, primary females produced an average of 10.4 offspring in their lifetime, of which 8.7 survived to adulthood, suggesting that primaries gain a benefit from having a secondary present in the nest (Mann–Whitney U test: $U = 15.90$, $P = 0.019$; Fig. 3).

To compare the per capita direct fitness benefits of each reproductive strategy, lifetime reproductive success calculations were based on average brood production of two females, since social colonies all had two females. Based on observed clutch sizes and brood survival rates in solitary and social nests, one solitary female nesting independently would have an average lifetime reproductive success of 7.5 brood. In social colonies, a primary and a secondary female together had a total lifetime brood production of 8.7. When correcting for the fact that there were two adult females in social colonies, their per capita brood production was 4.35. Given the observed estimates of clutch size and brood survival, solitary females had greater per capita direct lifetime reproductive success than social females (Fig. 3).

Figure 1. Rates of (a) brood production and (b) brood survival among solitary nesters, social primaries and social secondaries of *Ceratina australensis*. Different letters above the bars indicate statistical significance among reproductive strategies.

Figure 2. Intracolony relatedness observed between social females and expected based on haplodiploid relatedness for putative two-female relationships. The top histogram (observed social primary to social secondary relatedness, black bars) is for

Inclusive Fitness of Solitary and Social Individuals

Combining the brood sizes of each reproductive strategy (Fig. 1) with the genetic relatedness of social sisters and solitary reproductives to their offspring (Table 1), we calculated the relative inclusive fitness of each strategy, based on brood reaching adulthood. The benefit (b) of having a secondary female at the nest is the difference in the surviving numbers of brood between solitary nests (7.5 brood) and social colonies (8.7 brood). When correcting for the fact that there were two reproductive periods, $b = 0.6$ additional offspring surviving per brood period.

The inclusive fitness of primary females was calculated as the total offspring produced by an average primary female in the first brood ($c = 8.7/2 = 4.35$), multiplied by her relatedness to those offspring ($r_o = 0.5$), plus the offspring produced by the primary female in the second brood ($c = 4.25$), multiplied by her relatedness to those offspring ($r_o = 0.5$) and also multiplied by the probability that the secondary female does not inherit the nest ($1 -$ probability of nest inheritance, ca. 0.83).

The inclusive fitness of secondary females was calculated as the number of extra individuals contributed to the social nest in the first brood (over and above what the primary female might have produced on her own, $b = 0.6$), multiplied by their average relatedness to those brood ($r_k = 0.375$), plus the extra individuals contributed by the secondary female in the second brood ($b = 0.6$), multiplied by her relatedness to those brood ($r_k = 0.375$) and also multiplied by the probability that the secondary female does not inherit the nest (0.83), plus the offspring produced by the secondary female upon inheriting the nest ($c = 3.75$) multiplied by her relatedness to those offspring ($r_o = 0.5$) and also multiplied by the probability that she inherits the nest (0.17).

This then was compared with the total offspring produced by an average solitary female in the first brood ($c = 3.75$), multiplied by her relatedness to those offspring ($r_o = 0.5$), plus the offspring produced by the solitary female in the second brood ($c = 3.75$), multiplied by her relatedness to those offspring ($r_o = 0.5$) and also multiplied by the probability that the solitary female survives to the second brood (0.87; Rehan et al., 2010). Consequently, secondary females had an inclusive fitness of 0.73 and females reproducing solitarily had a much greater direct fitness of 3.51. Social primaries had an inclusive fitness of 3.98.

DISCUSSION

Social colonies in *C. australensis* form when two sisters remain together in their natal nest. Social females were predicted to have greater fitness than solitary reproductives, because primaries receive help, which should allow them to reproduce at a higher rate and secondaries should be able to compensate for their loss of direct fitness by increasing their inclusive fitness. However, we observed that the per capita lifetime reproductive success of solitary nesters was almost twice that of social nesters (Fig. 3). Some indirect fitness benefits are accrued by secondary females as a result of remaining to help their sister, the social primary, raise more offspring to adulthood. However, the size of this indirect fitness benefit did not compensate for the reduced direct fitness of secondary females. In another hymenopteran species where inclusive fitness has been carefully estimated (Leadbeater et al., 2011), delayed direct benefits explain why social nesting persists in the absence of inclusive fitness benefits, but in our study both the

calculated pairwise values using 11 loci and 13 colonies. Remaining histograms (grey bars) are simulated values based on the same number of alleles and allele frequencies as for the empirical data, but specific pedigree relationships.

Table 1
Intracolony relatedness (r) estimates for *Ceratina australensis* based on 11 polymorphic allozyme loci

| Class	Relationship	Expected r	Observed r	N	n
Solitary	Mother–daughter	0.5	0.616 (0.468–0.763)	13	59
	Mother–son	1.0	0.824 (0.593–1.056)	9	18
	Full sisters	0.75	0.715 (0.587–0.843)	14	77
Social	Full sisters	0.75	0.790 (0.696–0.885)	13	26

N: number of colonies; *n*: number of individuals. The observed mother–offspring, mother–daughter, mother–son and full sister relatedness estimates (95% confidence intervals) are based on solitary mothers and their offspring. Expected *r* estimates are based on monandrous and monogynous, haplodiploid regression relatedness, which for males are twice the classical life-for-life estimates (Bourke & Franks, 1995). The life-for-life mother–son relatedness is 0.5. Estimates were calculated using the computer program Relatedness 4.2 (Queller & Goodnight, 1989).

observed direct fitness and inclusive fitness for social secondaries were lower than for solitary females. In our study the higher fitness observed for solitary females implies that solitary nesting is expected to spread at the expense of social nesting. This might help explain why the frequency of social nesting is so low, but it does not explain why a low level of social nesting has persisted in this species since the earliest published records from the 1950s (Michener, 1962; and discussed below).

One potentially confounding factor in this and other census-based studies is that some solitary nests may have been social nests from which one female had departed, leading to our over-estimating the fitness and frequency of solitary nesting in the population. The fitness implications of social females disbanding prior to reproduction and their nests being deemed solitary when in reality they originated as social colonies are examined in Fig. 4. Estimates of false solitary nests were calculated by discounting the solitary female and increasing the secondary female's inclusive fitness by the percentage difference from observed values (Fig. 4): inclusive fitness of solitary female = observed inclusive fitness × (1 − percentage of false solitary nests); inclusive fitness of secondary female = observed inclusive fitness × (1 + percentage of false solitary nests). If 66% of solitary nests were originally social colonies, in which one female departed prior to reproduction, then social secondaries could have greater inclusive fitness than solitary females in this species. However, these rates of abandonment are far higher than the observed rate of nest orphaning, which is 3% of all brood-rearing nests (Rehan et al., 2010) and 13% of all nests surveyed, including overwintering and adult assemblages (Rehan et al., 2010). These low values of orphaning, observed across all nest categories, suggest that once females establish colonies, they are strongly nest loyal and rarely abandon nests upon initiating
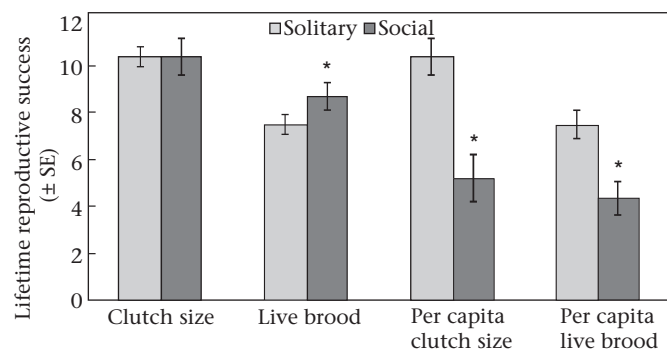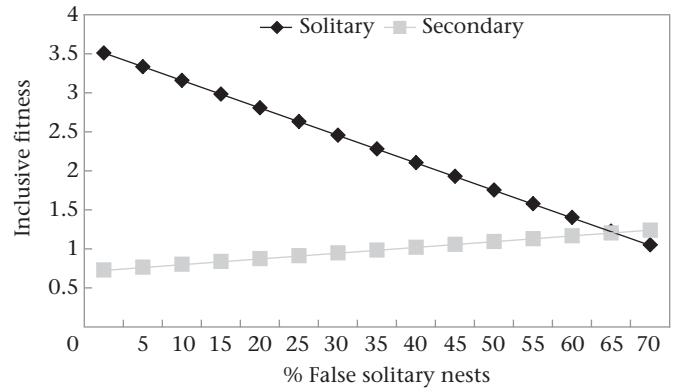
Figure 4. Implications of false solitary nests: whether solitary nests were formerly social colonies in which one female had left the nest could not be empirically measured in this study. The observed inclusive fitness of each reproductive strategy is shown as zero. As the percentage of false solitary nests (i.e. those potentially originating as two-female social colonies) increases, the inclusive fitness of solitary females decreases and that of social females increases. If 66% of all social nests were falsely deemed solitary, then a social secondary female would have greater inclusive fitness benefits than a solitary nesting female in the population.

reproduction in a stem. Our large sample sizes and prolonged collection periods provide assurance that the proportion of falsely identified solitary nests is too low in this species to negate our findings that, for *C. australensis*, solitary nesting is on average more advantageous than social nesting.

Alternative Explanations for Social Group Formation

In the face of such low direct and indirect fitness components for social secondaries in *C. australensis*, two mechanisms that might explain social groups need to be considered, namely helper subfertility and manipulation of subordinate helpers by dominant reproductives. First, the subfertility hypothesis posits that some individuals are less fecund and, therefore, they may be more likely to stay at the natal nest because they can realize higher fitness by helping than by nesting alone (Craig, 1983). Since secondary females were capable of reproducing in the absence of the social primary and were able to produce similar brood sizes to solitary females, subordinate behaviour cannot be attributed to subfertility. There is presently no evidence supporting the subfertility hypothesis in a facultatively social bee or wasp (Field & Foster, 1999; Smith, Kapheim, O'Donnell, & Wcislo, 2009; this study). Second, helping behaviour may result from social competition (Michener, 1974). In other primitively social bees, manipulation of subordinate helpers by dominant reproductives is often attributed to age- and size-based social hierarchies (Alexander, 1974; Hogendoorn & Velthuis, 1999). In this study, we found no signs of these predictors, as females were full sisters, with no consistent differences in body size, morphology or fat body size (Rehan et al., 2010, 2011). Physical manipulation via agonistic interactions has never been observed between cohabiting reproductive females in any *Ceratina* species studied to date (Sakagami & Maeta, 1977, 1995), although there is evidence for aggression in postreproductive assemblages (Rehan & Richards, 2013). Maternal manipulation has been posited to explain worker subordinance in the obligately social halictid bee, *Lasioglossum malachurum* (Richards et al., 2005). Queens of this species produce a first brood of workers; although workers do not accrue enough indirect fitness benefits to explain why they remain at the natal nest, the queen maximizes her inclusive fitness benefits through production of subordinate daughters. In *C. australensis*, maternal manipulation to produce two social sisters is precluded

Figure 3. Lifetime reproductive success estimates for solitary nests (one female) and social nests (two females) in *Ceratina australensis*. Asterisks denote statistical significance between solitary and social nests (Mann–Whitney *U* test: *P* < 0.05).

given the observed lifetime reproductive success and fitness estimates. Solitary females have greater per capita direct lifetime reproductive success than social females (Fig. 3). Moreover, a mother producing two solitary daughters would reap fitness benefits from two daughters each with an inclusive fitness of 3.51 (7.02 in total). Mothers producing two social daughters would have a reduced inclusive fitness with primary and secondary daughter contributing 3.98 and 0.73, respectively (4.71 in total).

The Implications of Dispersal for Social Potential

The cost of dispersal in *C. australensis* is unknown, but it is unlikely to be high, given that around two-thirds of all colonies are newly initiated each season (Rehan et al., 2010). Our estimates of relative inclusive fitness for solitary nesting females and social secondaries were 3.51 and 0.73, respectively. To estimate the cost of dispersal for solitary females, we discounted their inclusive fitness by the percentage mortality of dispersing females (Supplementary Fig. S1): inclusive fitness of solitary female = observed inclusive fitness × (1 − percentage mortality of dispersing female). This means that if costs of dispersal were sufficient to explain remaining at the nest as a secondary, survival of the dispersing solitary female would have to be about 20% that of a secondary remaining at her natal nest; in other words, dispersing would have to entail an ~79% risk of mortality (Fig. S1). Such a high value seems extremely unlikely given that suitable nesting substrates are abundant and dispersal represents only a small fraction of the time that solitary females subsequently spend rearing their brood. Nest substrate limitation is also not a plausible explanation for sociality in this species as the majority of nests are newly founded each season (66%; Rehan et al., 2010) and unoccupied stems that are suitable for nesting were always common (Rehan et al., 2010). However, the frequency of nest reuse is highly correlated with the frequency of social nesting in this and other *Ceratina* species (Johnson, 1988; Katayama & Maeta, 1979; Kislow, 1976; Rehan, Richards, & Schwarz, 2009; Sakagami & Maeta, 1977). In other words, social nesting might be influenced by dispersal patterns (Johnstone, Cant, & Field, 2012; Wild & Koykka, 2014).

Dispersal prior to brood rearing has strong implications for limiting social behaviour as it disbands groups. After eclosion, all *C. australensis* offspring must either disperse to find and construct a new nest, or remain at their natal nest and reuse it for an additional season. We found that social colonies of *C. australensis* comprise full sisters that remain at the natal nest, while dispersing females become solitary reproductives. The prevalence of social colonies in reused nests (Sakagami & Maeta, 1977, 1987, 1995) suggests that, in *Ceratina*, social colonies predominantly arise when females remain in a natal nest rather than joining a new nest. In contrast, North American *Ceratina* species have never been observed reusing nest substrates and do not form social colonies (Chandler, 1975; Kislow, 1976; Rehan & Richards, 2010a). *Ceratina flavipes* in Japan disperse and initiate new nests in autumn (Sakagami & Maeta, 1977) and only rarely (0.1% of nests collected) form social colonies in the wild (Sakagami & Maeta, 1987). Conversely, their Japanese sister species, *Ceratina japonica*, does not disperse prior to overwintering and frequently forms social colonies in reused nests (31%; Sakagami & Maeta, 1987). The latter two species were studied in sympatry, suggesting that local environmental conditions may be far less important in determining the selection for group living than latent genetic differences in any tendency for dispersal.

Reproductive Success and Direct Fitness

In addition to the cost of dispersal, the role of brood mortality and the effects of natural enemies at the nest are known to be strong selective agents on the fitness of social versus solitary reproduction (Lin & Michener, 1972; Smith et al., 2007; Zammit et al., 2008). In this study, differences in the observed brood parasitism rates resulted in lower brood survival for solitary females. If parasite pressure were to increase brood mortality for solitary nesters from the observed 28% (72% brood survival) to approximately 60% (40% brood survival), the lifetime reproductive success of solitary nests would decrease to the point where it would equal that of social females. However, if parasite pressure increased at the same rate for solitary and social colonies, there would be no point at which lifetime reproductive success of social females would exceed solitary reproductives.

Ceratina australensis were not observed during the 4-year study period to experience the level of parasite pressure required for mutual benefits to explain the formation of social colonies, as social females had lower fitness than solitary reproductives. For intermittent parasitism to maintain social nesting at the consistent rate of 13% observed in *C. australensis* (Rehan et al., 2010), then once every 2 years parasites would have to kill 92% of solitary brood. This projection is three times the observed brood mortality. It is possible that parasite pressure varies hugely over this bee's range or over longer periods of time, such that brood parasitism rates observed in our study over four brood rearing seasons were atypically low. If solitary colonies were continuously extirpated in surrounding populations, then the frequency of social nesting might increase considerably, as seen in allodapine bees (Schwarz et al., 2007; Schwarz, Tierney, Rehan, Chenoweth, & Cooper, 2011).

Cooperative Behaviour and Indirect Fitness

In this study we found no per capita benefit to group living for social colonies. Despite greater brood survival associated with group living (Rehan et al., 2010), per capita brood productivity was greatly reduced as a function of group living for social females. One explanation for the reduced brood production of social colonies is that it simply reflects the ergonomic limitations imposed by nest architecture. *Ceratina* construct a single linear burrow, with no central brood-rearing cavity or side branches in which two females can construct brood cells, provision and lay eggs concurrently. Nest architecture has marked effects on sociality in wood-dwelling bees. Social nesting is associated with the construction of branched nests in large carpenter bees (genus *Xylocopa*; Michener, 1990). Twig-nesting sweat bees (genus *Megalopta*) are capable of producing secondary nest tunnels and can access all brood cell chambers to concurrently work on multiple brood cells (Wcislo et al., 2004). The omission of brood cells facilitates concurrent provisioning and oviposition and coincides with the ubiquitous sociality found in the allodapine bees (Schwarz, 1988). In contrast, studies on manueliine carpenter bees (genus *Manuelia*; Flores-Prado, Chiappa, & Niemeyer, 2008) and the small carpenter bees (genus *Ceratina*; Sakagami & Laroca, 1971) suggest that short, linear nests are not conducive to cooperative nesting, and the nest architecture of wasps is also known to constrain colony size and social organization (Hansell, 1996; Turillazzi, 1989).

Conclusions

Our results indicate that inclusive fitness benefits of being a social secondary do not meet the conditions of Hamilton's rule. Importantly, Michener (1962) studied *C. australensis* in the 1950s and also found a low level of social nesting, and that means that low levels of social nesting in this species have persisted for over 100 generations, suggesting a stable social polymorphism. In our fitness estimates, indirect fitness comprised only a small benefit of social nesting. Our data indicate a very high level of relatedness between

primary and secondary females, as high as any estimate of intra-colony relatedness for social Hymenoptera entailing full-sister relationships between females without any appreciable effect of multiple mating. Despite the high level of relatedness, we have no evidence that secondaries play a worker-like role, and while their presence has a positive effect on brood survival, this is not enough to compensate for the brood production lost by virtue of two socially nesting bees producing a number of offspring equivalent to the number produced by a single, solitarily nesting female. We argue that in many species with simple forms of sociality, life history traits such as nest reuse and natal philopatry are key selective factors for the origins and maintenance of social living (Helms Cahan, Blumstein, Sundstrom, Liebig, & Griffin, 2002).

Empirical data and a consideration of likely long-term environmental variability suggest that being a social secondary can be favoured under certain conditions, including limited reproductive opportunities away from the natal nest (e.g. Schwarz et al., 2011), and this could be sufficient to explain the low levels of social nesting observed. However, in fitness estimates for C. australensis, indirect fitness comprised only a small benefit of social nesting. These results are similar to those observed in cooperatively breeding pied kingfishers, Ceryle rudis, in which breeding is superior to helping, but helping relatives is superior to doing nothing (Reyer, 1984). Although sociality has led to the great ecological success of some highly social lineages, including the termites, ants and honeybees (Wilson, 1971), most animals, insects and Hymenoptera remain solitary. It is widely thought that traits like natal philopatry are necessary preconditions to the evolution of cooperative breeding itself (Bourke, 2011; Helms Cahan et al., 2002; Wilson, 1971). Natal philopatry can produce low levels of social behaviour under conditions where Hamilton's rule would predict no cooperation (Nonacs, 2011). Phylogenetic inertia for preconditions such as natal philopatry could allow for the establishment of social groups (Rehan et al., 2012), after which the elaboration of more complex forms of sociality could evolve with enhanced benefits for helpers at the nest that are potentially in line with Hamilton's rule (Nonacs, 2011). Here we provide the demographic data to demonstrate that even in a facultatively social insect, social organization may be disadvantageous in terms of lifetime reproductive success, a scenario that should limit the spread of this trait, and even promote evolutionary reversions to solitary behaviour, as observed in this and other primitively social bee lineages (Wcislo & Danforth, 1997; Rehan et al., 2012). Future work on this and other Ceratina species will reveal genetic, life history and ecological correlates with transitions in social evolution and their potential causes.

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Supplementary Material

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