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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.

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