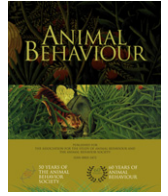


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Reproductive aggression and nestmate recognition in a subsocial bee

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In social contexts, the ability to recognize and discriminate among individuals is advantageous, because it allows individuals to adjust their behaviour so as to enhance both individual and group fitness. Eusocial insects have finely developed mechanisms of discrimination that promote many kinds of social interactions, but discrimination may also be adaptive in noneusocial species, including solitary ones. Physical traits such as reproductive status influence rates of aggression and discrimination, permitting individuals to share common resources and nesting sites and to cooperatively care for offspring, while excluding potential aggressors or social parasites. In this study, we examined reproductive aggression and nestmate recognition in a subsocial species of small carpenter bee, *Ceratina calcarata*, using circle tube behavioural assays. Not only does this subsocial bee show nestmate recognition, but there is seasonal variation in aggression that correlates with seasonal variation in reproductive status, illustrating that both aggressive behaviour and the consequences of nestmate recognition are context dependent. Females that were actively reproductive (ovaries fully developed) were more aggressive than pre-reproductive (ovaries undeveloped) or post-reproductive females (ovaries resorbed). Females altered their behaviour when interacting with nestmates versus non-nestmates. As in most social Hymenoptera, agonistic behaviour was observed to be greatest between unfamiliar, reproductively active individuals. However, post-reproductive females were tolerant towards unfamiliar females. During the natural adult cohabitation phase of the nesting cycle (the mature brood phase), mothers were aggressive towards daughters, whereas same generation pairs of nestmates or non-nestmates showed no signs of aggression. These results indicate that this subsocial bee species does possess the ability to recognize nestmates but the consequences of recognition vary seasonally, sometimes resulting in greater aggression towards nestmates than towards non-nestmates.

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The ability to discriminate among individuals with different social characteristics is a prerequisite to many kinds of social behaviour, including territoriality, pair bonding, care of young, maintenance of social hierarchies and colony defence (Fletcher & Michener 1987). Discrimination involves a minimum of two individuals, a cue bearer and a cue perceiver. Depending on the degree of similarity between the perceived cue and a learned template, the cue perceiver assesses the other individual and either treats it tolerantly or attacks it (Ribbands 1954; Bell 1974; Lacy & Sherman 1983; Gamboa et al. 1987b; Moritz & Neumann 2004; Kudo et al. 2007). Recognition of nestmates as well as other aspects of social status is indicated when perceivers react differently to different classes of individuals. In social bees and wasps, nestmate recognition is most easily inferred when familiar individuals are

more tolerant and unfamiliar individuals are more aggressive (Benest 1976; Greenberg 1981; Pabalan et al. 2000). However, the context of interactions between perceivers and cue bearers also matters, as recognition can result in different outcomes depending on the cues presented and upon the current situation. For instance, in the primitively eusocial sweat bee, *Lasioglossum zephyrum* (Hymenoptera: Halictidae), females distinguish not only familiar versus unfamiliar individuals, but also the degree of relatedness between females, and whether they are queens or workers (Breed et al. 1978). In two other sweat bees (*Lasioglossum figueresi* and *Halictus ligatus*), ovarian status influences reactions: females with larger ovaries are more aggressive whereas bees with smaller ovaries show more avoidance (Wcislo 1997; Pabalan et al. 2000). Therefore, in studies of behavioural interactions that might indicate nestmate recognition, it is important to also investigate context dependence.

An outstanding feature of the social insects is their frequent and elaborate cooperative behaviour, which depends on accurate discrimination between colony-mates and aliens (Hölldobler & Wilson

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2008). Nestmate recognition has been posited as a precursor trait for the evolution of complex sociality (Breed et al. 1978; Flores Prado et al. 2008; Richards & Packer 2010). In social contexts, discrimination among individuals is clearly advantageous, because it allows individuals to adjust their behaviour so as to enhance both individual and group fitness (Hamilton 1972; Gamboa et al. 1987a). As a result, previous studies of recognition in bees and wasps have largely focused on obligately eusocial species, testing the complementary predictions that adult females should show tolerant or cooperative behaviour towards nestmates and intolerant or aggressive behaviour towards non-nestmates (Bell 1974; Shellman-Reeve & Gamboa 1984; Breed & Page 1991; Buchwald & Breed 2005; Kudo et al. 2007). However, the ability to discriminate between familiar versus unfamiliar individuals or between nestmates and non-nestmates may have adaptive functions in other contexts as well. Nestmate recognition is likely to occur in solitary, subsocial and facultatively social species in which there exist opportunities for repeated behavioural interactions among adults. For instance, discrimination of unfamiliar adults might be helpful when nesting females face conspecific nest parasitism (Field 1992; Hogendoorn & Leys 1993), which can occur in bees and wasps of any social type.

Although behavioural interactions among individuals in obligately solitary and obligately eusocial bees have been well studied (Breed et al. 1978, 2007; McConnell-Garner & Kukuk 1997; Buchwald & Breed 2005; Packer 2006; Flores Prado et al. 2008), subsocial and incipiently social species have received less attention (Wcislo 1997; Arneson & Wcislo 2003; Peso & Richards 2010). Subsocial bees are informative species for elucidating the intermediate evolutionary steps in transitions from solitary antecedents to eusociality (Linksvayer & Wade 2005; Wilson 2008). Subsocial bees are typified by nest loyalty, adult longevity and prolonged cohabitation, all necessary preconditions for solitary lineages to evolve more complex social traits (Tallamy & Wood 1986; Crespi 1994; Costa 2006; Wilson 2008). Since a likely evolutionary route between solitary and eusocial behaviour involves a subsocial intermediate, empirical data on intraspecific variation in the behavioural profiles of subsocial species can be used to test the hypothesis that natural variation in the behavioural propensities of solitary and subsocial species might

provide the phenotypic plasticity from which social behaviour can evolve (West-Eberhard 1967; Linksvayer & Wade 2005).

The small carpenter bee, *Ceratina calcarata* (Hymenoptera: Apidae), is a subsocial species endemic to eastern North America; its colony cycle and social structure are both well understood (Johnson 1988; Rehan & Richards 2010a, b). Unlike highly eusocial, caste-differentiated species such as honeybees (Hymenoptera: Apidae), *C. calcarata* is subsocial, having neither morphological castes nor reproductive division of labour. *Ceratina calcarata* females are long-lived and nest loyal, and provide care to their offspring throughout development and even into adulthood (Rehan & Richards 2010b). In spring, overwintered females emerge from their hibernacula, dispersing to construct new nests in twigs and stems. 'Active brood nests' are those in the first phase of brood production and contain the reproductively active mother bee and developing brood of various ages (Fig. 1a). The active brood phase generally lasts from May to June. When females complete oviposition in early to late July, the nest enters the 'full brood' phase. The mother becomes reproductively inactive but remains in the nest to guard against predators and parasites, periodically inspecting and interacting with her brood (Fig. 1b). From late July to early August, the brood begin to eclose as adults. During this 'mature brood' phase, mothers interact with young adult offspring of both sexes. Many of these remain within the natal nest until the following spring (Fig. 1c), but some adult brood disperse to hibernacula elsewhere. During the mature brood phase, all females are reproductively inactive but of different generations. Very few, if any, mothers survive a second winter to reproduce in a second season (Rehan & Richards 2010a).

The prolonged nesting cycle of *C. calcarata* provides an excellent opportunity to track how sociodemographic status of the nest influences behaviours considered to be important precursors to sociality, including nestmate recognition. The first objective of this study was to determine the role of seasonal variation and socio-demographic status in behavioural interactions between females of *C. calcarata*. We used circle tubes to assay the behaviour of females collected at different points in the cycle to compare reproductively active versus post-reproductive non-nestmate mothers, and post-reproductive mothers versus pre-reproductive non-nestmate

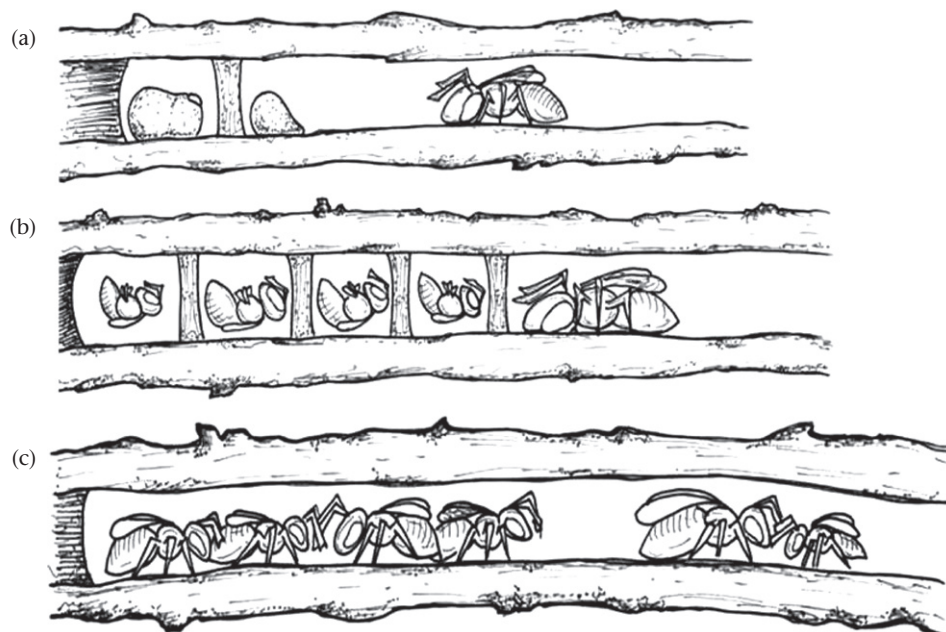


Figure 1. *Ceratina calcarata* nesting biology. (a) Active brood nest with reproductive mother actively foraging and ovipositing eggs. (b) Full brood nest with post-reproductive mother guarding the nest entrance as offspring develop in brood cells. (c) Mature brood nest with post-reproductive mother and callow offspring cohabiting.

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