



Experimentally induced alloparental care in a solitary carpenter bee



Vern Lewis¹, Miriam H. Richards*

Department of Biological Sciences, Brock University, St Catharines, ON, Canada

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Alloparenting, in which adults help to raise nondescendent offspring, is the hallmark of both cooperatively breeding and eusocial animal groups. Previous studies of the small carpenter bee, *Ceratina calcarata*, showed that mothers sometimes produce very small daughters, reminiscent of eusocial workers, suggesting retention of a complex social trait, alloparenting, in this secondarily solitary bee species. We tested the hypothesis that small daughters can act as alloparents by removing mothers from nests just prior to brood emergence, creating conditions under which small daughters should behave as alloparents. In 25 of 43 orphaned nests, a daughter took over the mother's role, foraging for pollen to feed her siblings. Alloparenting never occurred in control nests with surviving mothers. Alloparenting also did not occur when mothers disappeared before brood emerged as adults, as this invariably resulted in complete brood mortality. A second experiment demonstrated that post-eclosion feeding is necessary for overwintering survival. The expression of alloparenting in experimental nests suggests that alloparents could represent maternal insurance to ensure that adult offspring are fed before winter, and that alloparents could achieve indirect fitness from sibling care through assured fitness returns. However, complete nest failure in orphaned control nests demonstrates that brood only survive if their mother survives as well, which obviates the need for alloparenting. Therefore, alloparenting behaviour appears to represent the retention of an ancestral social trait that appears to have no current adaptive benefit in circumstances that highly favour solitary nesting and maternal brood care.

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Many kinds of insects and other small invertebrates display parental behaviour, caring for offspring after they hatch, sometimes past the stage at which offspring become nutritionally independent (Costa, 2006; Tallamy & Wood, 1986). In addition to parental care, there is also alloparental care in lineages as diverse as beetles, thrips, aphids, termites, ants, wasps and bees (Costa, 2006): groups of adults raise offspring together, with at least some adults acting as alloparents, caring for brood that are not their own. In invertebrates, groups that include alloparents are generally referred to as eusocial, with workers being the alloparents. Alloparenting also occurs in vertebrates (mammals, birds and fish), in cooperatively breeding societies that are very similar to the primitively eusocial societies of insects (Clutton-Brock, 2016). Most studies of alloparenting and its social evolutionary context focus on species that exemplify evolutionary transitions from solitary to social behaviour or on the maintenance of sociality after its origin. Indeed,

it has been argued that in the social insects (especially eusocial bees and wasps), social evolution can be conceptualized as the evolutionary splitting of ancestral, solitary maternal behaviour into two basic components, egg laying and brood care, that in eusocial descendants, represent behavioural specializations of mothers (queens) and alloparents (workers), respectively (West-Eberhard, 1987, 1996).

While there is considerable theoretical and empirical literature devoted to the origins and maintenance of sociality (Bourke, 2011, 2014), less attention has been paid to the conditions and processes that lead to evolutionary reversals from ancestral sociality to derived solitary behaviour. In secondarily solitary species, complex social traits such as alloparenting, cooperation, manipulation and division of labour have been replaced by simple parenting. Reversion to solitary behaviour may or may not involve 'reversing the evolutionary tape' of events that occurred when sociality evolved from its solitary antecedents. Do solitary animals with social ancestors retain the ability to express ancestral social behaviours, or are these behaviours extinguished during evolutionary transitions? If social traits are retained, under what circumstances are they likely to be expressed? These questions are interesting not only for understanding the behaviour of reversed solitary species

* Correspondence: M. H. Richards, Department of Biological Sciences, Brock University, St Catharines, ON L2S 3A1, Canada.

E-mail address: mrichards@brocku.ca (M. H. Richards).

¹ V. Lewis is now at the Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada.

themselves, but also for understanding the interplay between direct and indirect fitness components in shaping social evolution in animals. Since most social animals live in kin groups, a major focus of social evolutionary theory is on the interplay between direct and indirect components of fitness, with the latter increasing in importance as helping evolves (Bourke, 2014; Hamilton, 1964). In evolutionary reversals to solitary behaviour, it must be true that reproductive fitness contracts to its direct components only. By studying reversed solitary species, we may shed light not only on behavioural evolution, but also on the ecological factors that can lead to solitary behaviour being selected over social behaviour.

Arguably, the best animal models for investigating the factors and processes involved in evolutionary transitions back and forth between solitary and social behaviour are the bees (Apoidea). The evolutionary lability of bees has resulted in a huge diversity of social types forms, from small, low-skew casteless societies in which adult females share a nest but each produces her own offspring, to enormous colonies in which one queen monopolizes egg laying while thousands of workers labour to raise her offspring (Dew, Tierney, & Schwarz, 2015; Michener, 2007; Schwarz, Richards, & Danforth, 2007). Phylogenetic studies of bees indicate multiple independent origins of eusociality and alloparenting behaviour and even more frequent reversions to solitary behaviour (Cardinal & Danforth, 2011; Cronin, 2004; Gibbs, Brady, Kanda, & Danforth, 2012). Under many conditions, social nesting and alloparental behaviour confer higher fitness than solitary reproduction, but under other conditions, the opposite occurs, with solitary maternal behaviour conferring higher fitness than social reproduction and alloparenting (Rehan, Schwarz, & Richards, 2011).

Species that represent reversals to solitary behaviour were first identified using phylogenetic studies of the sweat bee family, Halictidae (Danforth, Sauquet, & Packer, 1999, 2003; Packer, 2000; Richards, 1994). To our knowledge, only one study has then investigated the extent to which secondarily solitary species retain ancestral traits related to social behaviour. Plateaux-Quénu (2008) compared maternal behaviour of ancestrally solitary, secondarily solitary and eusocial sweat bees. Ancestrally solitary bees provision their brood cells, then close them, and do not subsequently reopen them to inspect them during development, whereas primitively eusocial species open brood cells to inspect their brood (also see Quiñones & Wcislo, 2015), suggesting that inspection evolved after the transition to eusociality. Secondarily solitary species also open and inspect their brood cells (Plateaux-Quénu, 2008), suggesting that they lost social traits such as group living, alloparental care and reproductive division of labour but did not lose brood cell inspection behaviour. Evolutionary reversion to solitary behaviour involved only partial 'rewinding of the evolutionary tape' of events that previously led from solitary to social behaviour.

Bee species representing reversals to solitary behaviour have recently been identified by phylogenetic studies in the small carpenter bees (genus *Ceratina*, family Apidae) (Rehan, Leys, & Schwarz, 2012). Until very recently, this genus was considered to be mostly solitary, with a few facultatively social species involving multifemale nesting and possible alloparental care. When alloparental behaviour was induced in laboratory experiments in which females were forced to nest together, it was interpreted in light of an assumption that *Ceratina* is ancestrally solitary (Sakagami & Maeta, 1977, 1984, 1987). However, with expanding numbers of behaviourally studied species (Rehan, Richards, & Schwarz, 2009, 2010), it is now believed that social nesting is quite widespread and that *Ceratina* is ancestrally social (Rehan et al., 2012). Thus, species previously regarded as models for the evolutionary origins of sociality from solitary ancestors more likely represent models for evolutionary reversals to solitary behaviour and should be ideal

models for investigating the extent to which secondarily solitary species retain the potential for social nesting and alloparental care.

In the current study, we focus on a behaviourally well-studied small carpenter bee recently identified as representing an evolutionary reversion to solitary behaviour (Rehan et al., 2012). Detailed demographic and behavioural studies of *Ceratina calcarata* in two different localities in eastern North America indicate that solitary nest founding is ubiquitous and reinforced by considerable aggressiveness when females encounter each other during the spring nest-founding period (Johnson, 1990; Rehan & Richards, 2010a, 2010b, 2013). Mothers produce a single brood per year, which they provision, care for and guard until the young reach adulthood. Brood production entails considerable costs for mothers, the most obvious being accumulating wing wear, which lowers the efficiency of flight and the mothers' ability to carry pollen to their nests (Cartar, 1992; Foster & Cartar, 2011; Johnson & Cartar, 2014; O'Neill, Delphia, & Pitts-Singer, 2015). As a result, brood body size declines as mothers' wings wear out, with older offspring being larger than younger ones. An intriguing exception to this rule occurs with the first one or two offspring, which are often (but not always) very small daughters (Rehan & Richards, 2010b). Several lines of evidence demonstrate that the production of small eldest daughters is not due to environmental constraints (Rehan & Richards, 2010b; Vickruck, Rehan, Sheffield, & Richards, 2011). Small eldest daughters of small carpenter bees are reminiscent of the small eldest daughters that become workers in colonies of primitively eusocial sweat bees (Schwarz et al., 2007). This suggests that the small daughters of carpenter bees could be alloparents that care for younger siblings (Rehan & Richards, 2010b). If so, then alloparenting would represent retention of a complex social trait retained from a social ancestor with worker-like helpers.

In the current study, we tested the hypothesis that in the secondarily solitary species *C. calcarata*, small daughters can be induced to behave as alloparents that care for younger siblings. We reasoned that if post-eclosion feeding of adult offspring is critical to their overwintering survival, then alloparenting behaviour would most likely be inducible if mothers were unavailable to feed their adult offspring. We carried out a field experiment in which mothers were removed from their nests, so that newly emerged adult offspring would have to leave the nest to feed themselves or wait to be fed by one of their nestmates. We made three major predictions: (1) alloparenting would be inducible; (2) alloparenting would be more frequent in experimentally orphaned nests than in control nests where mothers could forage; and (3) alloparents would be smaller than their siblings. We also compared foraging effort of mothers and alloparents to roughly estimate the costs of reproduction from the point of view of both mothers and alloparents (Bourke, 2014; Linksvayer & Wade, 2005).

METHODS

Life History of Ceratina calcarata

Ceratina calcarata adults overwinter in their natal nests or in overwintering burrows (hibernacula) in twigs; in spring, they disperse and mate. Females search for suitable twigs or stems in which to construct their nests. After gnawing a tunnel longitudinally through the interior pith, a mother constructs one brood cell at a time, provisioning each with a loaf of pollen and nectar, laying an egg on top and closing the cell. After completing her brood, a mother remains in the nest, usually guarding the entrance by blocking it with her abdomen, but she also opens brood cells to inspect and care for developing juveniles (Rehan & Richards, 2010a). After the brood emerge as adults, many remain in the natal nest, which becomes a hibernaculum, but some disperse to

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