



Social interactions and their connection to aggression and ovarian development in orphaned worker bumblebees (*Bombus impatiens*)

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ABSTRACT

This study examines the social dynamics of reproductive conflict. Orphaned worker bumblebees (*Bombus impatiens*) with comparatively high or low levels of social activity were paired to determine whether aggression and reproduction could be traced to earlier social interactions. The workers were paired according to their levels of social activity (a socially active + another socially active worker, socially active + socially inactive, and two socially inactive workers). The presence or absence of brood was also manipulated. The absence of brood increased both aggression and ovarian development, suggesting that aggression and reproduction are associated or that there is a third variable that affects both. Socially active pairs were significantly more aggressive: here, social activity can be taken as an early indicator of aggression. No such effect, however, was obtained on ovarian development as the socially active pairs did not differ on their degree of ovarian development compared to the others. Within the socially active + socially inactive pairs, the socially active worker did not have more developed ovaries and was not more aggressive than her socially inactive partner. Results highlight that environmental conditions (the absence of brood) can predict ovarian development and although social activity can be observed prior to aggression, differences in aggression do not translate into differences in ovarian development under these conditions.

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1. Introduction

Bumblebee workers retain their reproductive capabilities and have the potential to produce male offspring. Nevertheless, through most of the colony life cycle they forego reproduction in favour of rearing the queen's offspring (Sladen, 1989). When worker oviposition (egg-laying) does occur, only a subset of workers become reproductive, becoming 'false' or pseudo queens (van Doorn and Heringa, 1986; van Doorn, 1987; van Honk and Hogeweg, 1981). They are given this label because they cease foraging and only lay eggs in a way reminiscent of the behaviour of queens. A form of reproductive competition is hypothesized to occur that will distinguish the reproductive workers from the non-reproductive ones and that this competition is expressed through aggressive and social interactions (Bourke, 1988a; Heinze, 2008). In ants (*Harpagoxenus sublaevis*) and wasps (*Ropalidia marginata*), for example, rigid social hierarchies are created with a single, reproductive queen. If the queen is removed from the nest, aggression is observed between the highest-ranked socially active workers to establish their status as a reproductive (*H. sublaevis*, Bourke,

1988b; *R. marginata*, Premnath et al., 1995). Similar suggestions are made with respect to bumblebees, specifically that aggression and characteristic social interactions differentiate a reproductive worker from a non-reproductive worker. This is based on the finding that social interactions and aggression coincide with ovarian development (*Bombus terrestris*, Alaux et al., 2004a; Bloch et al., 1996; *Bombus bifarius*, Free, 1955; *Bombus bimaculatus*, Pomeroy, 1981; *B. terrestris*, Duchateau, 1989; van Doorn, 1989; *B. bifarius*, Foster et al., 2004).

The relationship between ovarian development and aggression may not be as clear in *Bombus impatiens* compared to other species of *Bombus*. Although *B. impatiens* are similar to other species of bumblebee, e.g. similar patterns of worker ovarian development compared to *B. terrestris* workers (Cnaani et al., 2002), there are differences, e.g. a proportionally smaller number of reproductive workers in a colony (Cnaani et al., 2002). Additionally, in a recent study (Sibbald and Plowright, 2013) in which the behaviour of pairs of orphaned workers (i.e. queenless workers) was monitored 5–11 days after the bees were placed together, the more aggressive bee in a pair did not lay significantly more eggs than the less aggressive one. Moreover, the bee that laid more eggs in a pair did not show more aggression than the bee that laid fewer eggs. This may suggest that under conditions of unlimited access to food, aggression may be ineffective at suppressing reproduction in another or it serves another purpose in worker pairs. In other eusocial species,

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for example, aggression is used to encourage foraging and other nest duties (Lamba et al., 2008; Clarke and Faulkes, 2001), is a necessary behaviour to encourage the ovarian development in itself (Lamba et al., 2007) or reflects a combination of functions (Clarke and Faulkes, 2001; Premnath et al., 1995). Conversely, the lack of an association between aggression and reproductive suppression in *B. impatiens* pairs may be indicative of other variables that have a more predominant role in bumblebee pairs.

Social interactions were not measured in our previous study (Sibbald and Plowright, 2013) on aggression and reproduction in pairs of orphaned bumblebees. As workers were randomly paired, it is likely that bees of differing degrees of social activity were paired together. The reproductively dominant queen rarely retreats from social interactions (van Honk and Hogeweg, 1981) and as such these social interactions may be a component of reproductive competition in workers. In the present study, in addition to obtaining measures of aggression and reproduction, we recorded social interactions as soon as workers were paired to determine whether these interactions could serve as an early indicator of reproductive conflict. Moreover, we harnessed this variable by experimentally assigning workers to groups depending on their levels of social activity. If social interactions serve to mitigate future aggression, i.e. to resolve behavioural contests, one possible outcome of this study would be that when workers are unequal in their levels of socially activity (as opposed to both being socially active or inactive) then future aggression would be reduced. We used the definition of 'social activities' (Kardile and Gadagkar, 2003; van Doorn, 1989; van Doorn and Heringa, 1986; van Honk and Hogeweg, 1981), which consisted of contacts between workers which were measured at a time typically before aggression (e.g. head-butting) and reproduction. Topographically, the social activities were distinguishable from aggressive and reproductive behaviours.

The presence of brood is predicted to play a significant role in reproductive competition. Based on the research, however, its relationship is mixed. Brood interactions and feeding, for example, are positively associated with oviposition (Foster et al., 2004) and ovarian development (Duchateau and Velthuis, 1989). Aggression is also more likely to occur in areas of the nest where the brood are located (such as in *Leptothorax allardycei*, Cole, 1988). Nevertheless, these previous studies were correlational and therefore specific conclusions regarding causation cannot be made. In an experimental manipulation of the presence versus absence of brood, in contrast, aggression and oviposition were more likely to co-occur in pairs placed without brood compared to pairs with brood (Sibbald and Plowright, 2013). This suggests that brood presence inhibits aggression that occurs during egg-laying. Conditions that further induce aggression (i.e. pairing two socially active bees together) may accentuate the effect of brood.

This study was performed on a common North American species of bumblebee, *B. impatiens*, to address three main questions: (1) Does pairing orphaned worker bumblebees according to their levels of social activity affect their levels of aggression? (2) Does it also affect their ovarian development? (3) Does the presence of brood, when experimentally manipulated, promote or inhibit aggression and ovarian development?

2. Methods

2.1. Colonies

Two commercial *B. impatiens* colonies supplied by BioBest, Biological Systems and three *B. impatiens* colonies derived from wild-caught queens and reared according to the procedure of Plowright and Jay (1966) were used. All colonies were maintained in the laboratory under identical conditions and in compliance

with institutional guidelines regarding the ethical care for animals. The workers were collected from their colonies between July and December, 2008.

All bees were marked by glueing coloured, numbered tags (Opalit Plättchen, The Bee Works, Orillia, ON) onto the thorax. The groups were supplied with food ad libitum: 50% honey-water solution and pollen collected by honeybees that is mixed with honey-water solution to form a uniform dough. Pollen is necessary for ovarian development (Duchateau and Velthuis, 1989).

2.2. Target workers

Target workers (the objects of study) were 118 *B. impatiens* orphaned workers from the five queen-right colonies. Workers that were within 12 h of emergence from their cocoon (defined as 'callow workers'; bees not having full colouration and having curved wings) were randomly selected. Callow workers were chosen to ensure that workers were of comparable age. The callow workers were kept in isolation for 12 days to allow enough time for possible ovarian development (as previous research has found it takes an average of 11.8 days for single *B. impatiens* workers to lay eggs (Sibbald, 2007, unpublished data)). Isolated callow workers that were later paired have also been used in other research and found to display behaviours consistent with larger groups and older bees (Amsalem and Hefetz, 2010). They also develop mature ovaries comparable to those callows that were allowed social contact (Cnaani et al., 2007).

2.3. Behaviour testers

To manipulate levels of social activity across pairs of target workers, it was necessary to assess these levels first. To this end, nine *B. impatiens* adult workers of unknown age from three queen-right colonies (the two BioBest colonies, and one of the colonies derived from a wild-caught queen) were randomly selected as 'testers' of social interactions in the target workers. These testers were placed singly in nesting boxes. To ensure these testers had developed ovaries they were not used for behaviour testing until eggs were observed in their nest boxes.

2.4. Apparatus

Once the bees were removed from their colonies they were housed in wooden nest boxes (10.2 cm × 10.2 cm × 5.1 cm) under humid conditions at 30 °C. The box was lined with honeybee wax to allow for a surface for egg-cup building. For the With Brood group, eggs were gathered from queen-right colonies and placed in the nesting box. The box was connected to a second nest box where a glass feeder tube was located. Glass plates covered the top of the boxes to allow for easy observation. The laboratory was illuminated by a combination of fluorescent light fixtures and natural light. Digital video recordings were made on a JVC Hard Disc Camcorder positioned directly over the nest box.

2.5. Assessment period

After their 12 days of isolation, the target workers' social activity was assessed. The target workers were placed in a new nesting box with one of three behaviour tester bees. Their behaviour was observed for five minutes and all social interactions and aggression were coded. A score of the degree with which the target workers initiated interactions versus retreated from them was calculated and workers were categorized as either socially active (SA) or socially inactive (SI). This was based on van Doorn and Heringa (1986) as well as van Honk and Hogeweg, 1981 definition of dominant social interactions of the bumblebee. Aggressive interactions were rare,

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