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Dufour's gland secretion, sterility and foraging behavior: Correlated behavior traits in bumblebee workers

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ABSTRACT

Bombus terrestris colonies go through two major phases: the "pre-competition phase" in which the queen is the sole reproducer and aggression is rare, and the "competition phase" in which workers aggressively compete over reproduction. Conflicts over reproduction are partially regulated by a group of octyl esters that are produced in Dufour's gland of reproductively subordinate workers and protect them from being aggressed. However, workers possess octyl esters even before overt aggression occurs, raising the question of why produce the ester-signal before it is functionally necessary?

In most insect societies, foragers show reduced aggression and low dominance rank. We hypothesize that ester production in *B. terrestris* is not only correlated with sterility but also with foraging, signaling cooperative behavior by subordinate workers. Such a signal helps to maintain social organization, reduce the cost of fights between reproductives and helpers, and increase colony productivity, enabling subordinates to gain greater inclusive fitness. We demonstrate that foragers produce larger amounts of esters compared to non-foragers, and that their amounts positively correlate with foraging efforts. We further suggest that task performance, potential fecundity, and aggression are interlinked, and that worker–worker interactions are involved in regulating foraging behavior.

B. terrestris, being an intermediate phase between primitive and derived eusocial insects, provides an excellent model for understanding the evolution of early phases of eusociality. Our results, combined with those in primitively eusocial wasps, suggest that at early stages of social evolution, reproduction was regulated by a "primordial division of labor", that comprised foragers and reproducers, which further evolved to a more complex division of labor, a hallmark of eusociality.

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1. Introduction

Cooperative behavior is a hallmark of social insect societies. It helps to maintain the social organization and serves not only the reproductive individuals, but is also in the interest of subordinate workers, since by performing tasks that augment colony productivity, they gain greater inclusive fitness (Hamilton, 1964, 1972; Hammond and Keller, 2004).

In many social insects, helping behavior, and particularly foraging, is done by subordinate, lower ranked non-reproductive females (Breed and Harrison, 1988; Hudson et al., 1987; Litte, 1981; Michener, 1974; Cant and Field, 2001, 2005; Foster et al., 2004; Molina and O'Donnell, 2009; Röseler and van Honk, 1990; de Souza et al., 2008). Studies in honeybee, where foraging behavior was extensively investigated, show that foraging is triggered by various stimuli at the individual- and colony-level and involves multiple changes in gene expression and hormonal levels (reviewed in Page et al., 2012). However, less attention was given to the different mechanisms regulating foraging in species that exhibit different level of sociality, and particularly to the differences between primitively eusocial insects, where females retain their full reproductive potential and there are no discrete worker and queen behavioral, physiological or morphological castes (Hunt, 2012), and highly eusocial insects where extreme reproductive skew exists as well as discrete castes and morphological differences between reproductives and helpers. Investigating the mechanisms regulating foraging in various species may provide an insight into the factors that may have led to the evolution of eusociality.

In primitively eusocial insects, foraging is often regulated by behavioral means, where aggression is directed towards the behaviorally subordinate females, manipulating them to forage (Hudson et al., 1987; Gamboa et al., 1990; Lamba et al., 2007, 2008),

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whereas in highly eusocial insects in which between-worker aggression is rare, foraging is often regulated through pheromones (Ping et al., 2011; Sumpter and Pratt, 2003). When foraging behavior is regulated by aggression, the outcome, in most of the cases, is that the foragers are precluded from egg laying. But, since aggression in such a context is not aimed at directly affecting reproduction, sterility is only a byproduct of regulating division of labor, and a way to increase inclusive fitness by subordinate workers that gain more fitness by helping relatives to rear offspring who carry shared genes than by direct reproduction (Chandrashekara and Gadagkar, 1992; Gamboa et al., 1990; Keeping, 1992; O'Donnell, 1998; Premnath et al., 1996). When foraging behavior is regulated through pheromones, foragers can either restrain their reproduction to gain more fitness in response to a cooperative signal (thus, foraging is the pheromone's prime target and sterility is a byproduct), or can be directed to relinquish reproduction and forage in a response to a manipulative signal (thus, the pheromone's prime target is the regulation of reproduction and foraging is the byproduct). However, since sterility and foraging in highly eusocial insects are often correlated, it is hard to determine which of the options prevails. For example, the transition in honeybee workers from in-nest activity to foraging is regulated by the queen-mandibular pheromone (Pankiw et al., 1998). This pheromonal effect is mediated through juvenile hormone (JH) levels, which are assumed to regulate both reproduction and cooperative behavior (Huang and Robinson, 1996; Robinson, 1987; Amdam and Omholt, 2003; Page et al., 2012), emphasizing the inter-relation between foraging behavior, reproduction and pheromones. In species where inter-colonial competition is pronounced, aggression may also be involved due to the interaction between foraging and aggressive behavior in primitively eusocial insects (Hudson et al., 1987; Lamba et al., 2007, 2008).

Bombus terrestris presents an excellent model to investigate the interplay between foraging, pheromones, reproduction and aggression since they represent an intermediate stage in the evolution of eusociality with regard to all of these aspects. For example, workers are sterile and cooperative during the first phase of life cycle (the "pre-competition phase"), but thereafter they aggressively compete with the queen and other workers over male production (the "competition phase") (Duchateau and Velthuis, 1988). Similarly to other primitive social insects, workers establish a dominance hierarchy using overt aggression (Amsalem and Hefetz, 2011; Amsalem et al., 2013), but subordinates also produce ester-sterility signals that somewhat mitigates aggression (Amsalem et al., 2009; Amsalem and Hefetz, 2010) bringing it to the level that is more common in highly eusocial insects.

The ester-sterility signals are produced in worker Dufour's gland, which is a source of pheromones that mediate reproductive competition in several social insect species. For example, in the queenless ponerine ant *Dinoponera quadriceps* the alpha female marks her rival with Dufour's gland secretion to elicit attack by other workers (Monnin et al., 2002), or in the honey bee where the secretion signals fertility and triggers aggression in the competition between queenless workers (Dor et al., 2005; Malka et al., 2008). In *B. terrestris* the ester component of the secretion operates as sterility signal that is exclusively produced by workers and negatively correlate with their ovarian activation (Amsalem et al., 2009). Subordinate workers that produce higher amount of these esters were found to receive less aggression from the dominant worker (Amsalem and Hefetz, 2010).

In *B. terrestris* the competition phase in normal colonies is similar to queenless conditions in that it is characterized by aggression, worker oviposition and mutual egg eating (Duchateau and Velthuis, 1989). During this phase, approximately 64% of the workers activate their ovaries but only 38% eventually lay eggs, although all workers are physiologically capable of doing so (Alaux et al., 2004; Duchateau and Velthuis, 1989). Hence, even under this chaotic condition, some social organization, supported mainly by the non-reproducing workers that forage and care for the brood, is maintained. This allows the eggs laid by the dominant workers to fully develop into males (Alaux et al., 2004; Bloch and Hefetz, 1999). Moreover, division of labor in *B. terrestris*, unlike honeybees that display temporal polyethism (Robinson, 1987; Seeley, 1982), is rather weak and does not seem to be regulated either through JH levels, or dominance, or age, albeit older bees are more likely to care for brood (Geva et al., 2005; Jandt and Dornhaus, 2009; O'donnell et al., 2000; Yerushalmi et al., 2006). Several studies have indicated that larger *B. terrestris* workers tend to become foragers while smaller ones tend to be nurses and tend the larvae (Goulson et al., 2002; Michener, 1974). House-bees also tend to have the highest chances to reproduce during the competition phase (van Doorn and Heringa, 1986). On the other hand, foraging behavior was found to strongly correlate with lower ovarian development (Duchateau and Velthuis, 1989; van Honk and Hogeweg, 1981; Röseler and van Honk, 1990).

Aggressive behavior in *B. terrestris* is a prevalent phenomenon, shaping many aspects of their social organization. However, even under the seemingly chaotic conditions during the competition phase, reproductive division of labor among workers is maintained by subordinates advertising their sterility and diverting any aggression away from them (Amsalem and Hefetz, 2010). In addition, reproductive-subordinate workers produce esters already during the pre-competition phase before the onset of overt aggression in the colony, and in even higher amounts compared to sterile workers during the competition phase and under queenless conditions (Amsalem et al., 2009). Thus, ester production may communicate additional information such as behavioral or physiological state, including brood care and foraging. Such a signal may be especially adaptive in primitively eusocial insects where task allocation and reproductive conflict are confounded and worker–worker aggression prevails, as in bumblebee colonies.

The aim of the current study was to test whether the ester-sterility signal conveys dual information; sterility and undertaking the task of foraging. Advertising sterility signals to other workers that the producer is not a reproductive competitor and at the same time signals the producer's positive contribution to nest success (the foraging information). Such signaling confers a selective advantage, since it protects the signaling workers from aggression and thus is predicted to contribute to the total reproductive output of the colony. To address this question, we characterized bumblebee foragers in full-sized colonies and their foraging efforts with regard to their ovarian development, pheromone production, age, size and social phase. This question can also be placed into evolutionary perspective since bumblebees represent an intermediate phase between primitive and advanced eusocial insects, providing insight into the interrelation between correlated behaviors that may have led to the evolution of eusociality.

2. Methods

Four colonies of *B. terrestris* were obtained from the Yad Mordechai apiary, Israel, at the age of 3 days post emergence of the first worker: two colonies (A, B) during autumn 2010 and two (C, D) during spring 2011. These colonies were reared at Tel Aviv University and were initially maintained in the laboratory in nest boxes (23 × 23 × 10 cm) at a constant darkness, temperature of 30 °C and 60% humidity, and supplied *ad libitum* with a sugar solution and fresh pollen collected from honeybee colonies. Newly emerged workers were daily tagged for individual recognition. 20 days after first worker emergence, when colonies contained at least 30 workers, food was removed and the colonies were connected to the

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