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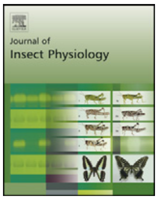

Reproductive plasticity in *Polistes* paper wasp workers and the evolutionary origins of sociality

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ABSTRACT

Regulatory pathways in solitary species provide the raw materials for the evolution of sociality. Therefore, comparing the mechanisms that mediate reproductive plasticity in social species and their solitary ancestors can provide insight into the evolutionary origin of sociality. In many solitary insects, the effect of juvenile hormone (JH) on fertility is mediated through the fat body; individuals in good physical condition show a stronger fertility response to JH than individuals in poor physical condition. Here, we test whether a similar, condition-dependent JH response mediates fertility in workers of the primitively eusocial *Polistes dominulus* wasps. We test how body weight, JH, and adult nutrition influence worker ovarian development. Both JH-treatment and adult nutrition dramatically increased ovarian development. Body weight also influenced ovarian development, as large workers developed more eggs than smaller workers. Body weight and fat are strongly linked in *P. dominulus* workers, so these results suggest that the fat-dependent JH responsiveness common in solitary insects is conserved in social wasps. The simple, ancestral relationship between reproductive investment and physical condition may facilitate cooperation by allowing workers to adaptively allocate energy into reproduction based on their probability of successfully becoming a queen.

1. Introduction

The evolution of sociality has long interested biologists (Lin and Michener, 1972; Wilson, 1971). Much research has focused on the selective costs and benefits of sacrificing independent reproduction to help rear the offspring of others (Andersson, 1984; Sherman et al., 1995). Less is known about the evolutionary origin of reproductive sacrifice within social groups and the physiological mechanisms that mediate variation in reproduction among group members.

It can be difficult to study the evolutionary origin of a behavior such as sociality. One valuable method is testing the mechanisms that underlie social behavior and comparing them with mechanisms found in solitary ancestors (Amdam et al., 2004; Hunt et al., 2007; West-Eberhard, 1996). Identifying the parallels between regulatory pathways present in social species and their solitary ancestors can provide insight into the origin of sociality, as the pathways present in solitary species provide the raw materials for social evolution.

One hypothesis for the origin of sociality is the 'ovarian groundplan hypothesis', which posits that the ovarian cycle in solitary insects provides the basis for social evolution (West-Eberhard, 1996; West-Eberhard, 2003). This hypothesis proposes that social and solitary insect behavior may be linked by juvenile hormone (JH) responsiveness. Specifically, reproductive plasticity in social insects may have originated via modification of the nutrition-dependent endocrine responsiveness that occurs in solitary insects (West-Eberhard, 1996). Many solitary insects show a nutrition-dependent response to juvenile hormone, JH. Fat body responds to JH by producing the yolk protein vitellogenin, so individuals in good physical condition develop more eggs in response to JH than individuals in poor physical condition (Engelmann, 1983; Nijhout, 1994; Wyatt and Davey, 1996). If the condition-dependent endocrine responsiveness that mediates reproductive plasticity in solitary species also regulates reproduction in social insects, individual condition is predicted to influence reproduction of social insect workers. However, this prediction has not been experimentally tested.

Although the role of JH responsiveness in the reproductive sacrifice of workers has not been tested, previous work suggests that condition-dependent JH response may influence reproduction in nest founding queens. *P. dominulus* foundresses form cooperative associations where the dominant foundress is the primary reproductive. Subordinate foundresses act much like workers; they forage and typically do not reproduce (Reeve, 1991; Röseler, 1991). The effect of JH on foundress fertility varies with individual condition. Large foundresses with facial patterns advertising high quality respond to JH by increasing their fertility, while small

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foundresses with facial patterns advertising low quality do not increase their fertility in response to JH (Tibbetts and Izzo, 2009). Body weight and advertised quality are associated with foundress dominance rank and reproduction (Reeve, 1991; Tibbetts and Dale, 2004), so these results indicate that the condition-dependent endocrine responsiveness of foundresses may be an adaptation that facilitates resource investment. Does a similar, condition-dependent mechanism mediate reproductive plasticity among workers?

We tested whether condition-dependent hormonal response mediates reproductive plasticity among *P. dominulus* workers. Specifically, we tested how adult feeding, body weight, and treatment with the JH analog methoprene influence worker reproductive potential. In addition, we confirmed that weight is associated with physical condition in *P. dominulus* workers by measuring the relationship between body weight and fat content.

2. Methods

2.1. Study system

Polistes wasps provide an interesting model for studying the evolution of sociality because there is plasticity in reproductive behavior within each caste that parallels the plasticity between castes. For example, some nest-founding *Polistes* paper wasp foundresses become the reproductive dominant, while others take a subordinate role and do not reproduce. Subordinate foundresses act much like workers. They care for the dominant's offspring instead of reproducing independently (Reeve, 1991; West-Eberhard, 1969). There is similar reproductive plasticity within paper wasp workers. Most workers care for the dominant's offspring and do not reproduce. However, some workers take over their natal nest or disperse to reproduce independently (Page et al., 1989; Strassmann, 1981; Tibbetts, 2007; Tibbetts and Huang, 2010).

Polistes are a primitively eusocial taxa that lacks discrete morphological castes, so the phenotypes of queens and workers overlap (O'Donnell, 1998; Tibbetts, 2006; Toth et al., 2009). As a result, defining the caste of a particular individual can be challenging. Definitions of 'queen' and 'worker' may vary across studies. For this study, we define workers as females that eclose from their nest in late June and July before the cohort of reproductive males. In temperate species, like *P. dominulus*, the first broods to eclose on a nest are typically non-reproductive foragers, workers. Early eclosing females can develop active ovaries and reproduce independently in the same year (O'Donnell, 1998; Solis and Strassmann, 1990) or they may enter early diapause and found nests the following year (Reeve et al., 1998; Tibbetts, 2007). As a result, they are sometimes called 'undifferentiated females' instead of 'workers'. However, the vast majority of early eclosing females in temperate species become non-reproductive foragers, so we will use the term 'worker' for simplicity. Females that eclose later in the season are idle females in reproductive diapause (idle females or gynes) (Mead et al., 1995; O'Donnell, 1998; Solis and Strassmann, 1990). Gynes mate, overwinter, and emerge the following year as nest founding females. Different factors may influence gyne reproduction, as individuals are in reproductive diapause (Hunt, 2007; Hunt et al., 2007). Therefore, this study does not examine gynes.

2.2. Experimental procedures

Single foundress *P. dominulus* nests were collected from the wild in June. The nest and foundress were transplanted into boxes in the lab and provided with water, sugar, and an *ad lib* diet of *Bombyx mori* and *Galleria mellonella* caterpillars. Nests experienced a natural day/night cycle that matched the outdoors and were kept at 25 °C. Nests were checked daily for worker eclosion from pupation. Individuals used in the experiment eclosed between June 25 and July 28, 2009. At eclosion, each new worker was removed from her nest, weighed, and placed in a individual deli cup with sugar and water. Individuals were removed on the day of eclosion to reduce the effects of nest social environment on reproduction. Workers were randomly assigned to treatment groups and experimental treatment of workers started the day after pupal eclosion. Workers experienced both a hormone treatment and a diet treatment. 123 individuals from 19 nests were included in the analysis.

2.2.1. Hormone treatment

Half the workers were treated with 5 μg methoprene in 1 μl acetone three times a week for two weeks. The other half the workers were treated with 1 μl acetone alone three times a week for two weeks as a control. Methoprene and acetone were topically applied to the thorax. Methoprene is a JH analog and previous studies using similar methods have shown that methoprene has behavioral and physiological effects similar to those of JH (Giray et al., 2005; O'Donnell and Jeanne, 1993; Robinson and Vargo, 1997). Further, methoprene acts in ways similar to JH at the cellular level (Ashok et al., 1998; Parthasarathy and Palli, 2009; Shemshedini and Wilson, 1990). The timing and amount of hormone treatment was chosen because it parallels previous work on reproduction in *P. dominulus* foundresses (Tibbetts and Izzo, 2009).

2.2.2. Diet treatment

Half the workers received no caterpillars, while the other half were given *B. mori* caterpillars three times a week during the treatments. Most of an adult wasps' diet is sugar, so the caterpillar treatment provided *ad lib* caterpillars. Workers typically ate some of each caterpillar, but did not entirely consume each caterpillar.

In sum, workers received one of four treatments: caterpillars and methoprene, caterpillars and acetone control, no caterpillars and methoprene, no caterpillars and acetone control. After two weeks, individuals were sacrificed and their ovarian development was assessed. The total length of all eggs was used as the measurement of ovarian development because this measure effectively captures variability across individuals.

2.3. Fat analysis

The relationship between worker weight and fat content was measured using workers that pupated in the wild. Adult workers were weighted on a scale accurate to 0.001 g three times and the average was used as the final weight. Then, abdominal fat was assessed using ether extraction, as most available fat body is in the abdomen (Arrese and Soulages, 2010). Abdomens were placed in fat free paper thimbles (Whatman), dried at 80 °C for three days, and weighed on a balance accurate to 0.0001 g. After weighing, the abdomens were extracted in diethyl ether for 24 h, washed in fresh diethyl ether, and dried for another 3 days at 80 °C. Following the second drying, abdomens were weighed again. Fat content was calculated from the difference between the dry mass and the dry fatless mass post extraction. 49 workers from 19 nests were included in this analysis.

2.4. Statistical analysis

Data were analyzed in SPSS v. 17. Data were analyzed using a mixed linear model. The dependent variable was ovarian development, which was log transformed prior to analysis. The