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Effect of Group Size on Ovarian Development in Bumblebee Workers (Hymenoptera: Apidae: Bombus)

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Isolated bumblebee workers, *Bombus impatiens* Cresson 1863, developed their ovaries to produce laying-sized eggs in 11 days, but did so 5 days faster in queenless groups of 2–12 that they came to dominate. In groups larger than pairs, reproductive dominance (as measured by oocyte length) was distributed continuously in a graded hierarchy, rather than dichotomously. In groups, workers at a particular dominance rank position developed larger oocytes as group size increased, indicating that a focal bee's stimulus for reproductive development depends on the number of other bees that are subordinate to it. Attempts to relate ovarian development to visible behavioral manifestations of dominance were inconclusive because antagonistic interactions were infrequent.

Key words: *Bombus impatiens* (Cresson 1863) – dominance hierarchy – oocyte – social isolation

CNAANI J, WONG A & THOMSON J D [Abtg Zool; Univ Toronto, Ont; Canada]: **Auswirkung der Gruppengröße auf die Entwicklung der Ovarien bei Hummel-Arbeiterinnen (Hymenoptera: Apidae: Bombus).** – Entomol Gener **29**(2/4): 305–314; Stuttgart 2007-01. – – – [Mitteilung]

Isolierte Hummel-Arbeiterinnen (*Bombus impatiens* Cresson 1863) entwickelten ihre Ovarien zur Produktion von legefertigen Eiern innerhalb von 11 Tagen. Wenn Arbeiterinnen eine königinnenlose Gruppe von 2–12 anderen Arbeiterinnen dominieren, dauerte diese Entwicklung jedoch nur 6 Tage. Bei Gruppengrößen >2 war die reproduktive Dominanz (quantifiziert als Länge der Oocyten) kontinuierlich in einer graduierten Hierarchie verteilt, und nicht in einer bimodalen Verteilung. Arbeiterinnen eines bestimmten Dominanzranges entwickelten größere Ovarien bei einer größeren Anzahl der Tiere innerhalb der Gruppe. Dies deutet darauf hin, daß der Stimulus für die reproduktive Entwicklung einer gegebenen Arbeiterin von der Zahl der Arbeiterinnen abhängt, die sich in der Hierarchie unter diesem Tier befinden. Der Versuch, die Ovarienentwicklung in Bezug zu sichtbaren dominanten Verhaltensmustern zu setzen, ergab keine eindeutigen Ergebnisse, da antagonistische Interaktionen selten waren.

Schlüsselbegriffe: *Bombus impatiens* (Cresson 1863) – Dominanzhierarchie – Oozyte – soziale Isolation

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1 Introduction

Although in many species of social insects the queen functions as a solitary individual during the period of founding the colony, social isolation is neither natural nor common for the workers. The behavioral and physiological effects of social isolation are poorly understood, and it is sometimes considered that highly eusocial insects are usually unable to live in complete isolation [e.g FRANKS & PARTRIDGE 1994]. Nevertheless, social isolation provides an important tool for studying the effects of the social environment on the physiological state of the individual. For example, BOULAY et al [2000, 2001] studied the role of the neurotransmitter octopamine in maintaining social cohesion between nest-mates in ant colonies. They socially isolated workers of the ant *Camponotus fellah* (Dalla Torre 1893), and showed that an increase in their trophallaxis rate after returning to the colony could be eliminated if the isolated individual was injected with octopamine.

If kept away from queens, newly emerged workers of the bumblebee species *Bombus impatiens* (Cresson 1863) can develop mature oocytes by the age of 7 days if they are held with other workers but not if they are isolated [CNAANI et al 2002]. The presence of other conspecific workers is essential: holding a bumblebee worker with a bumblebee male or with a honeybee worker [honeybee workers are used to promote egg laying by queens in commercial rearing of *Bombus terrestris* (Linnaeus 1758)] does not induce ovarian development. Bumblebee workers are known to develop a physiological hierarchy among themselves in which the reproductively dominant individuals inhibit ovarian development in the subordinates [BLOCH & HEFETZ 1999, DOORN 1989, HONK & HOGEWEG 1981]. Therefore, living in a group seems to have two contrasting effects on the reproductive system of the worker: being in a group is a stimulating factor for ovarian development, but at the same time it may lead to inhibition of ovarian development in subordinate individuals

If subordinate individuals show suppressed oogenesis when exposed to a dominant individual, why would an isolated individual, who is not exposed to any dominant-subordinate relationship, not develop her ovaries fully? Perhaps ovarian development is not only inhibited in the subordinate, but is also accelerated in the dominant. If so, changing the tempo of oogenesis may require a competitive social situation that initiates change through some sort of branching process that accelerates oogenesis in some group members while retarding it in others. (The terms 'accelerate' and 'retard' are used here in relation to the tempo of oogenesis in isolated individuals.)

The effects of worker-worker interactions on oogenesis are relevant to situations other than artificial queenless groups. In the typical development of *B terrestris* colonies, some workers start laying eggs at a stage termed the 'competition point'. From this point onward, dominant workers play an important role in inhibiting oogenesis in younger workers [BLOCH & HEFETZ 1999]. It remains unknown whether, and by what means, dominant-subordinate relationships between workers differ from queen-worker relationships.

The principal aim of this study is to better understand how social isolation affects oogenesis. Specifically, it is asked whether social isolation prevents ovarian development or only delays it. An attempt is made to identify the minimal duration of social interaction that is needed for the fastest ovarian development, and whether there is a critical age at which the interaction is important. The effect of group size on oogenesis is also examined. An attempt is made to relate the ovarian development of individuals to behavioral observations indicative of their dominance status within groups. Additionally, it is investigated whether social effects on oogenesis require free interaction of the bees or can be induced by airborne pheromones or antennal contact only.

2 Material and methods

2.1 Material

Bumblebee pupae were kindly provided by BioBest Biological Systems, Leamington, Ontario, Canada. The pupae were maintained in a rearing room at 28°C±2. Every day all emerged workers were collected, ensuring that all bees found in the pupa box at the next day are less than 24 hours old. The experiments were conducted in small plastic containers (diameter 4.5 cm; height 8 cm) with paper bottoms to absorb feces. Holes drilled in the container wall allowed ventilation. Each cage was stocked with 7ml of 50% sugar water in a small Petri-dish and about 1 g of pollen mixed with sugar water, sufficient to provide *ad lib* food for the duration of the experiments.

To estimate ovarian development, workers were dissected under a microscope, their ovaries removed, placed on a microscope slide, and the length of each terminal oocyte measured with a scaled ocular. The average length of the largest terminal oocyte in each of the two ovaries was used as an index for ovarian development [Cnaani et al 2002]. In addition, the radial cell in the front wing of each worker was also measured as an index of body size. To minimize the effect of size differences between workers occupying the same cage on the establishment of dominance, and possibly on differences in ovary size [Doorn 1989], it was attempted (by visual inspection) to select equal-sized workers when setting up a pair or group for testing. The ability of the experimenters to do this depended on the size distribution of workers available at the time.

2.2 Separation by screen

To verify whether social influences on oogenesis required physical contact, 2 newly emerged workers were placed in the same plastic container that was divided by wire screen. The workers could touch each other through the screen with their antennae or mouthparts, but could not occupy the same compartment. Trophallaxis is not known in bumblebees, so food exchange presumably did not occur. Each worker had her own unlimited supply of sugar water and pollen. The workers were dissected at 7 days and their oocytes measured.

2.3 Duration and timing of social isolation

To determine the duration of social interaction needed for maximal ovarian development, workers were placed in the plastic cages, either alone (isolated) or as an even-aged pair. Four types of experiments were conducted:

2.3.1 Early contact: Two newly emerged workers were put together and kept in social contact for a specified number of days, after which they were separated and isolated in different containers for the remainder of their first week. The contact periods were one, two, three, four, or five days.

2.3.2 Late contact: Newly emerged workers were initially placed in isolation (each worker in a different cage), then placed in pairs for a specified number of days for the remainder of their first week. The contact periods were two, three, four, or five days.

2.3.3 Mid-period contact: Workers were placed in pairs for one day only, on either the second day or the third day after emergence. During the rest of the first week, they were in isolation.

2.3.4 Extended isolation: Isolated workers were dissected at the ages of 3, 5, 7, 9, 11 and 13 days in order to assess whether ovarian development is prevented or just delayed.

2.4 Oocyte size in relation to the dominance hierarchy

The position of each individual worker within the dominance hierarchy was determined by observing behavior. Four groups of 2, 4, and 6 newly emerged workers of about the same body size were established in plastic cages (described above). Each individual in the group was uniquely marked by a colored plastic tag. Each group was observed for 30 min every day for 7 days. Dietary pollen is required for maturation of the oocytes, so one way of achieving behavioral dominance would be to monopolize the pollen ball. Therefore, the time each individual spent on the pollen ball was recorded, and it was determined which individuals engaged in aggressive interaction, and for each aggressive interaction, which individual retreated and which prevailed. Aggressive interactions included (1) incidents in which one bee rapidly approached another, threatening with open mandibles (often raising her forelegs), or (2) fights involving direct contact. A dominance index was calculated for each focal individual using the formula 1-[instances of retreat /total aggressive interactions] [BLOCH et al 1996].

To expand the range of group sizes examined, groups with 3, 4, 6 or 12 newly emerged workers were set up. After 7 days, all were dissected for measuring oocyte length.

3 Results

3.1 General worker size

Body size of *B impatiens* workers varied greatly: radial cells ranged from 1.9 to 3.1 mm, corresponding to body masses ranging from approximately 60 to 190mg. In pilot studies, radial cell length was significantly related to the mean length of the largest pair of oocytes (regression analysis, $r^2 = 0.4$, n = 27 $P<0.0004$). Therefore, the experiments reported here were restricted to a narrower range of radial cell lengths from 2.44–3.0mm (corresponding to body masses of 100–175mg). Furthermore, for statistical analysis of treatment effects on ovary size, ANCOVA with radial cell length as the covariate was used. The workers used in the experiments originated from pupae collected from different colonies over long periods of time. However, no heterogeneity in maximum oocyte length was found among experimental dates (which corresponded to different cohorts of pupae; ANCOVA with worker size as covariate, $F_{3,17} = 0.96$, $P = 0.43$).

Extended isolation did not prevent the maturation of the oocytes, but simply slowed the process (**Fig 1**). Although a dominant worker confined with a subordinate would have fully grown oocytes (approaching the size of ready-to-lay eggs, 2.24±0.6 mm, n = 22) within 7 days, oocytes of isolated workers reached only 0.76±0.6 mm (n = 11) by that age. However, the oocytes of isolated workers continued to grow and reached the length of 2.31±0.3 mm (n = 6) by the age of 11 days. Separation by a wire screen within a container had the same effect as complete isolation (oocyte length at 7 days 0.58±0.3 and 0.76±0.6 mm for workers separated by a screen and completely isolated, respectively; ANCOVA with worker size as covariate, $F_{1,14} = 1.21$, $P = 0.29$).

Social interaction during the first day only does not maximize the rate of ovarian development (**Fig 2**), but workers allowed to interact for the first 2 days of their life developed oocytes as large as those of workers that spent the whole 7 days together (2.21±0.41 (n = 5) and 2.24±0.6 (n = 22) mm for 2 days and 7 days of interaction; ANCOVA with worker size as covariate, $F_{1,24} = 0.1$, $P = 0.76$). However, 2 days of social interaction at the end of the first week (days 6 and 7) did not result in fully grown oocytes, although the mean oocyte length (1.5±0.6 mm, n = 6) was higher than in fully isolated workers (ANCOVA with worker size as covariate, $F_{1,25} = 4.6$, $p = 0.04$).

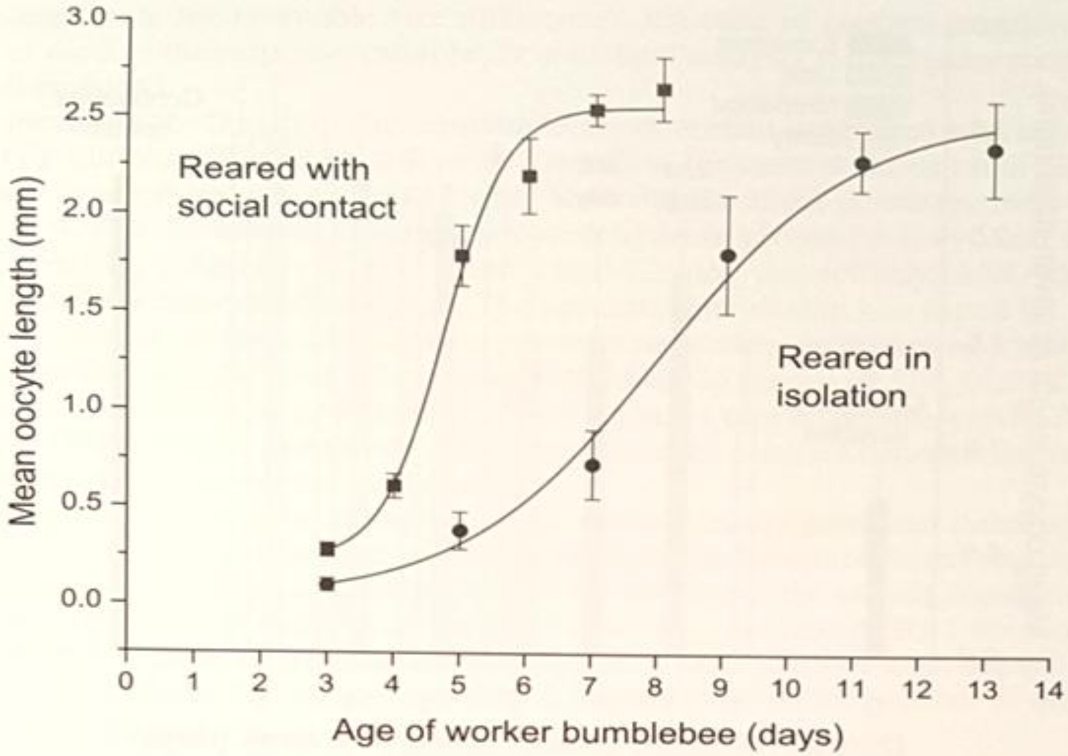
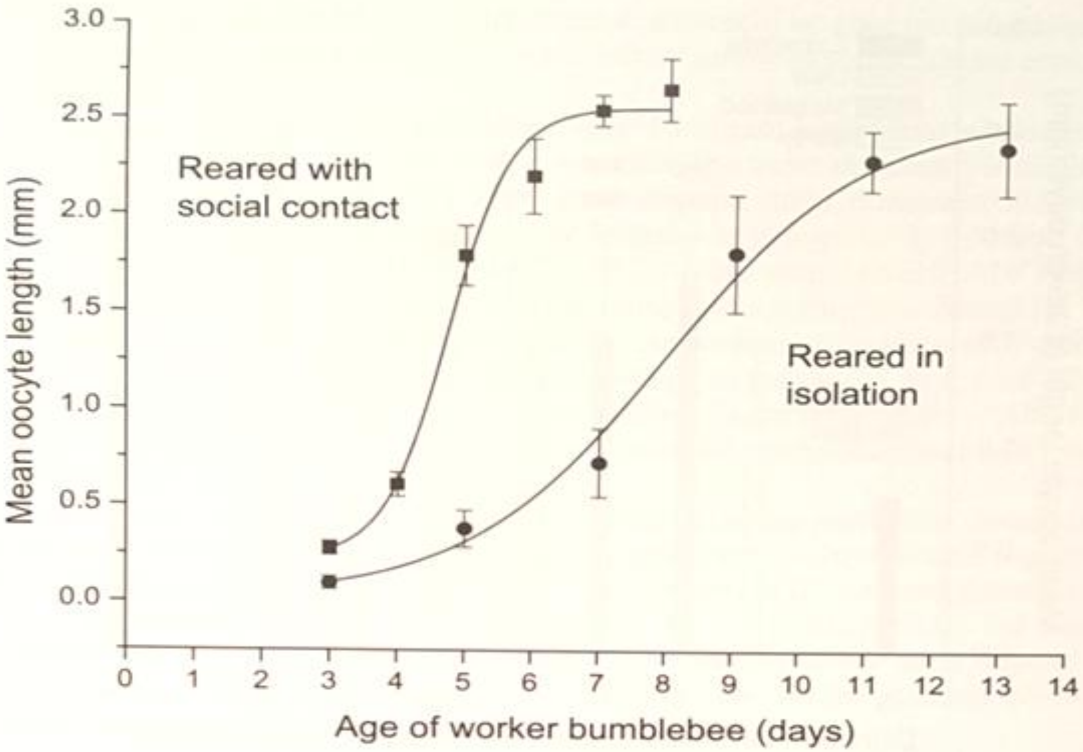


Fig 1: Effect of social environment on rate of oogenesis in bumblebees (Hymenoptera: Apidae: *Bombus impatiens* Cresson 1863). The data are for the reproductively dominant individual with each group (i.e, the individual with the largest oocytes). Squares denote mean (±SE) oocyte size in workers that had interaction with other workers; circles denote isolated workers. Data for workers with social contact from CNAANI et al [2002]; data for isolated workers, this study.

Workers exposed to social interaction only during the 2nd or the 3rd day of their life had slightly larger oocytes than workers exposed to social interaction during their first day only, and slightly smaller than workers exposed to two days of social interaction (1.8±0.4 and 1.5±1 mm for 2nd and 3rd day exposure, respectively). Those differences, however, were not significant (ANCOVA with worker size as covariate, $F_{3,18} = 1.3$, $P>0.29$).

3.2 Reproductive dominance in relation to behavioral dominance

Overt aggressive events were rare for most of the groups (fewer than 10 events per group in 10 out of 12 observed groups), preventing us from accurately specifying the dominance hierarchy by the ratio of attacks to retreats. The time an individual in a group spent on the pollen was highly variable, ranging from over 100min to less than 5 min out of the total 210min of observation. Within groups, the individual that spent the most time on the pollen tended to develop larger oocytes than the individual that spent the least time on the pollen, as indicated by the ratios of [(oocyte length of the bee with the most time on the pollen)/(oocyte length of bee with the least time on the pollen)]. These ratios (± SE) were 2.1±0.7, 6.5±5.6 and 18.5±11.2 times in groups of 2, 4 and 6 workers, respectively. Examining the data in other ways, the individual with the largest mean oocyte length was also the one who spent most time on the pollen in 2 out of 4 groups of two workers, 3 out of 4 groups of four workers, but in none of the 4 groups of six workers.



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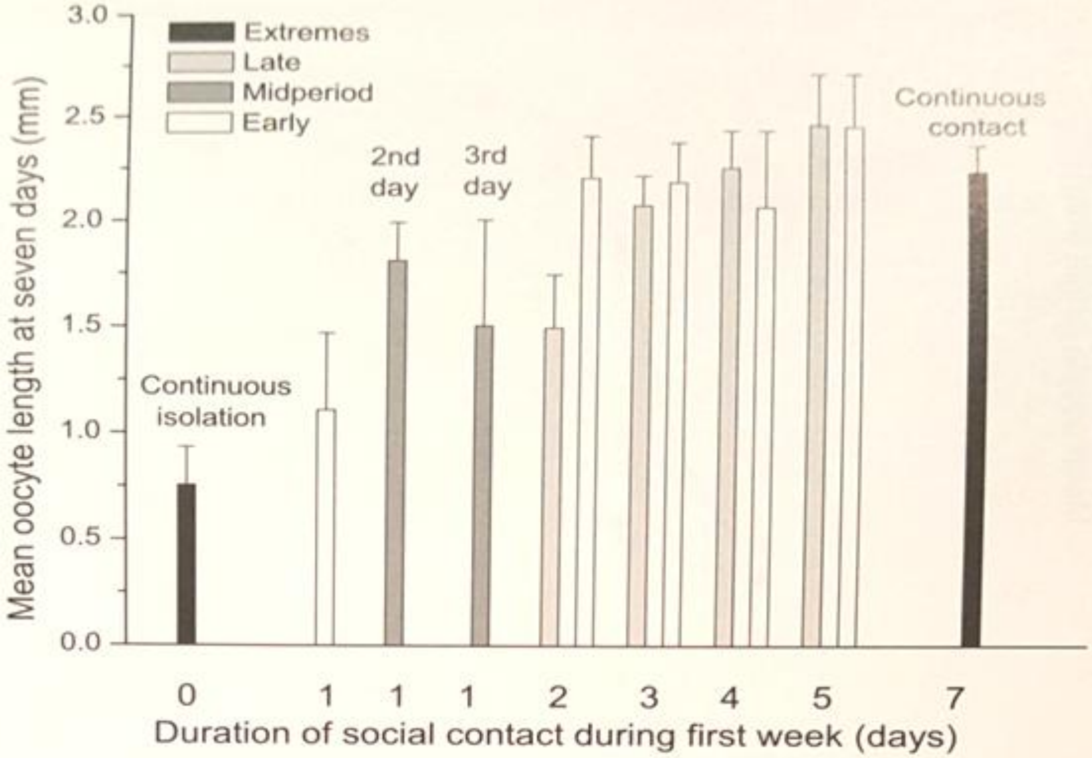

Fig 2: Mean (±SE) oocyte size for 7-day-old workers (Hymenoptera: Apidae: of *Bombus impatiens* Cresson 1863) that were exposed to different durations of interaction with another worker of the same age. Data are for the member of the pair that had larger oocytes. The exposure treatment (see definitions in text) is indicated by the shading of the bars: open bars = *Early contact*; light gray bars = *Late contact*; dark gray bars = *Mid-period contact*, with one bar for contact on day 2 and the other for day 3; the black bars at the extremes of the graph indicate bees that were kept in isolation throughout (left bar) or were kept in contact throughout (right bar). The different treatments are shown in one figure to indicate the general trend for oocyte development to increase with duration of social contact.

For a more inclusive test that took all the data into account, rather than only the extremes, each of the 12 groups was divided into two paired sub-groups, depending on whether each bee spent more or less time on the pollen than the median time for its group. The oocyte lengths of all the bees in each sub-group were summed; these sums were compared within each group to see which sub-group had achieved more oocyte development, and then used a sign test to ask whether the pollen-monopolizing sub-groups tended to outperform the pollen-excluded sub-groups in oocyte development. This happened in only 7 cases out of 12, suggesting that oocyte size is not related to the time spent on the pollen (χ^2=0.33, P=0.56).

3.3 Effect of worker number

As mentioned above, the behavioral observations were insufficient to establish a reliable dominance hierarchy based on contests among individuals. Therefore, henceforth only the physiological manifestation of reproductive dominance, as measured by oocyte size of an individual, relative to the others within its group, is considered. In a group of equal-sized workers, the individual with the largest oocyte would be considered the most dominant, and the one with the smallest oocytes as the least dominant.

To compensate for inevitable size differences, the ratio of [oocyte length/radial cell length] was used as the response variable for statistical analysis (after square root and arcsine transformation).

The mean oocyte length of the reproductively dominant individual was significantly affected by group size (**Fig 3**). In groups of 2 workers, the most dominant individuals had significantly smaller oocytes (2.2±0.12 mm) than did the most dominant individuals in groups of 3, 4, 6 or 12 workers (average oocyte lengths in groups of 3, 4, 6 and 12 workers were 2.5±0.18, 2.7±0.01, 2.7±0.11 and 2.6±0.22 mm, respectively, ANOVA, $F_{4,49} = 5.55$, $P = 0.0009$ with contrast analysis). The opposite relationship was found for the most subordinate workers. In this case, the most subordinate workers in groups of 2 workers had larger oocytes than did the most subordinate individuals in groups of 3, 4, 6 or 12 workers (1.6±0.15, 1.01±0.38, 0.83±0.14, 0.46±0.13 and 0.29±0.1 mm respectively; ANOVA, $F_{4,49} = 9.18$, $P<0.0001$). Larger groups, therefore, increased the contrast between dominant and subordinate bees with respect to oogenesis.

More particularly, ovarian development of workers in any particular dominance rank position increased with group size, as shown by significant positive linear regressions of oocyte length on group size: $F_{4,49} = 7.1$, $P<0.01$ for workers of the second dominance rank; $F_{3,26} = 6.86$, $P<0.014$ for workers of the third rank; $F_{2,21} = 6.29$, $P<0.02$ for workers of the fourth rank). That is, the ovarian development of a particular bee does depend on how many others rank above her, but beyond that, it depends also on the number of others that are subordinate to her.

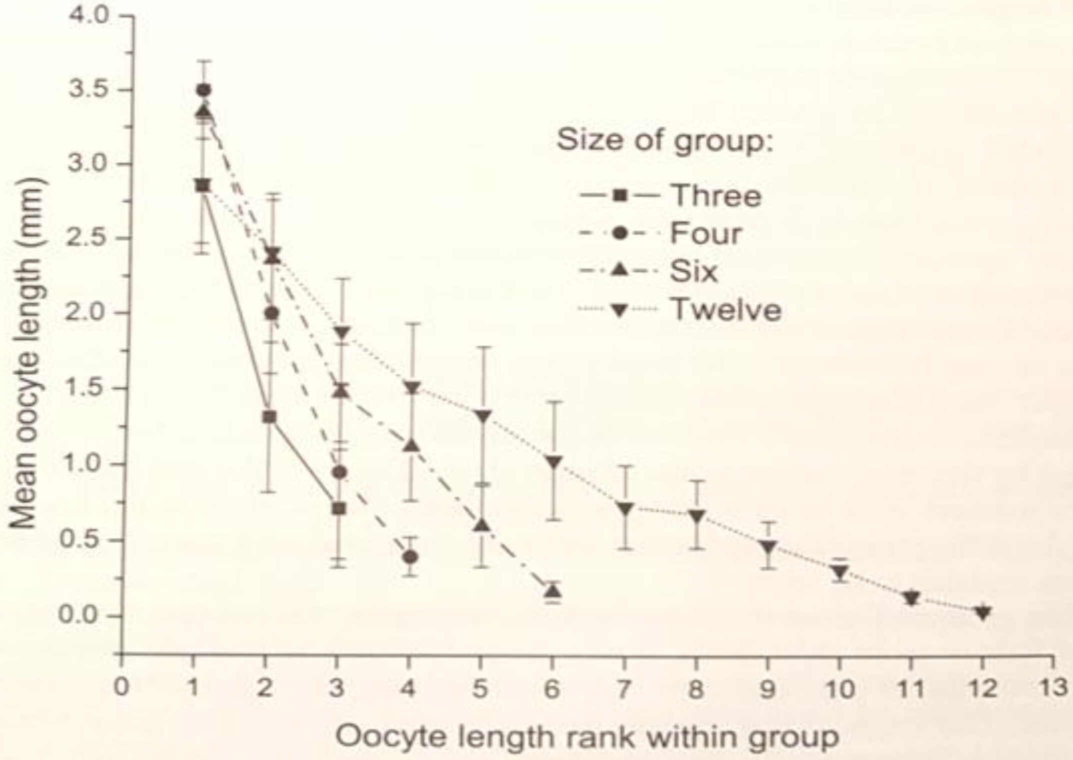

Fig 3: Oocyte length in 7-day-old workers (Hymenoptera: Apidae: *Bombus impatiens* Cresson 1863) workers that lived in groups of various sizes. Workers in each group were ranked according to the relative size of their oocytes (the first-ranked worker had the largest oocyte in its group, number 2 had the second largest oocyte).

4 Discussion

Social isolation does not prevent oogenesis. Isolated workers were able to produce full-sized eggs, ready to lay, by the age of 11 days, but being in a group stimulated the dominant workers to mature equally large eggs by the age of 7 days. By separating a pair of workers with screen, it was shown that full physical contact and interaction are needed for accelerated oogenesis; antennal contact or smelling another worker is not enough. It is not possible to speculate about probable mechanisms.

Oocyte growth curves for *B impatiens* [Cnaani et al 2002], as well as for *B terrestris* [Bloch et al 2000a], show that in workers with fully accelerated oogenesis, almost all oocyte growth occurs during days 4–7. It was shown that full acceleration can be achieved by exposure to another worker during this growth period (the last 3 days of the first week) or by exposure for at least two days before the growth period. This suggests that: (1) there is no sensitive period after which oogenesis cannot be accelerated, and (2) that the social interaction accelerates some developmental process related to the oogenesis but does not accelerate the oogenesis itself (because isolation after 2 days of contact, before oocyte growth started, still resulted in faster oogenesis). One such oogenesis-related process could be the activation of the corpora allata to synthesize juvenile hormone (JH) at a higher rate [Nijhout 1994, Tobe & Stay 1985]. It is tempting to explain the relation between social isolation and oogenesis by the effect of isolation on octopamine levels. As Boulay et al [2000] showed, social isolation can be associated with low octopamine levels. Moreover, there is evidence that octopamine activates the corpora allata to synthesize JH [Kaatz et al 1994, Rachinsky 1994, Roeder 1999], octopamine is also known to be elevated in dominant workers of *B terrestris* [Bloch et al 2000b]. These relationships between social isolation, octopamine level, and oogenesis need further investigation.

The attempt to relate behavioral dominance status to ovarian development was not successful, as the number of the observed interactions between the workers was too small to calculate meaningful dominance indices. This low level of aggressiveness between workers was somewhat surprising, since agonistic interactions between workers were observed in preliminary trials. It is possible, however, that aggression between individuals in *B impatiens* is generally lower than in *B terrestris*. Cnaani et al [2002], for example, were unable to observe any agonistic interaction between workers in queenright colonies of *B impatiens*, even at late stages of colony development when the queen's dominance is presumably fading. The occasional aggressive interaction that was observed, and the differences in rates of oogenesis among individuals in the same group, suggest that hierarchies do form among the workers, but that different methods would be needed to document this process by observation. Nevertheless, dominance need not be measured only by agonistic behavior. It can also be inferred by the reproductive status of individuals [Drews 1993] and thus, it is possible to refer to workers with faster oogenesis as dominant over workers with slow oogenesis. Whether the differences in reproductive status are correlated with some type of behavioral differences remains to be seen.

Within groups of more than two workers, oogenesis was not just 'fast' or 'slow'. In groups of four or more individuals, it was always possible to find one worker with fully developed oocytes, at least one with very small oocytes, and some with oocytes of intermediate size. This suggests that workers have different ranks in a continuous hierarchy and are not divided dichotomously into dominants and subordinates. Moreover, it was found that oocyte size of a worker of specific rank (2nd, 3rd, 4th … in the hierarchy) is affected by the number of individuals below her. For example, an individual that is the 3rd in group of 12 workers will have larger oocytes than individuals who are 3rd in a smaller group of 6, 4 or 3 workers.

This group-size effect could be the result of 'diluting' a dominant worker's inhibitory effect across a larger number of individuals in a larger group: as group size increases, the dominant individual loses its ability to control the subordinates. Such effects have long been known for primitively eusocial halictines; for example, see the report by STROHM & BORDON-HAUSER [2003] that documents the increased development of workers' ovaries in large colonies of *Lasioglossum malachurum* (Kirby 1802). It is also commonly recognized as a general problem in maintaining reproductive dominance in large societies [FLETCHER & ROSS 1985, REEVE & KELLER 2001]. On the other hand, as has been shown, oogenesis is subject not only to inhibition but probably also to acceleration. Is it possible that in groups of different sizes, individuals who are positioned in the same rank receive different levels of acceleration specifically because they dominate different numbers of subordinates? Answering such questions can clarify the regulation of ovarian development in social insect workers, and will give a better understanding of the social organization in the colony. It will require, though, better understanding of the neurophysiological and endocrine controls over ovarian development, and especially the neurophysiological changes that are associated with establishing social dominance.

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Once upon a time, bumblebees were a major model in evolutionary biology, largely because of the many genetically determined differences between and within species and populations, for example in their colour coats (see e.g the works by H FRIESE & F VON WAGNER, O VOGT, and WF REINIG in the first third of the 20th century). For a few decades, bumblebees took the back seat while *Drosophila* became the most powerful model for insect evolutionary genetics, and research on insect behaviour otherwise concentrated on the honeybee, *Apis mellifera*. In the 1970s, however, bumblebees become *the* model for studies into the adaptiveness of foraging behaviour, and their general availability from commercial bumblebee breeders since the 1990s has increased their popularity as model for studies in ecology and behaviour.

GOULSON's book covers several areas in which recent advances have been made, for example thermoregulation and socio-biology, mate-finding and natural enemies, foraging and pollination, as well as conservation. It provides a reasonably comprehensive account of these topics and is intelligible for the non-specialist, as well as being informative for the seasoned bee biologist. There is somewhat too much focus on the author's own work – roughly two-thirds of the figures are taken from GOULSON's research, while his original contribution to bumblebee behaviour and ecology is probably somewhat lower than this percentage. This appears to be reflected to some extent in the cited literature: in many cases a reference to significant earlier work is missing in the text, although some of the relevant papers do appear in the comprehensive reference list. However, the book does inspire curiosity and fascination for the biology of bumblebees, and is therefore successful in achieving one of its main goals – to raise awareness for the plight of the bumblebees in modern environments, and to help with their conservation.

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