CAUSES OF THE LACK OF DIAPAUSE IN BUMBLE BEE FEMALES (*Bombus Latr., Apoidea*)

M o n i k a F l i s z k i e w i c z

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S u m m a r y

The study was performed at the Chair of Economic Insects, Agricultural University, Poznań. The objective of the study was to determine the causes of the failure of bumble bee females to undergo diapause.

Ninety-two diapausing queens and 89 non-diapausing queens were reared in the laboratory. In addition, 40 naturally overwintered queens were caught for analysis. All queens were examined for the following characteristics: ovary size, volume and filling of spermathecae, and dry matter of the fat body.

Of the anatomical characteristics of the reproductive organs of bumble bee females that may have significantly affected the occurrence of diapause ovary length and filling of spermathecae were of prime importance. The mean values of those characteristics were significantly higher in diapausing queens than in non-diapausing queens. The mean length of both ovaries and the number of sperms in the spermathecae were significantly higher in naturally reared queens compared to those from the laboratory rearing which may have been the reflection of an imperfect understanding of the requirements of bumble bee colonies reared under laboratory conditions.

Ovary width and spermatheca volume have no influence on the occurrence of diapause in bumble bee females as no statistical differences for mean values of those characteristics were found in diapausing vs. non-diapausing queens.

The size of the fat body influences the occurrence of diapause. The diapausing queens developed a fat body with a significantly higher dry weight meaning that they were better prepared to survive the diapause than the non-diapausing queens.

Keywords: Bumble bees, diapause, ovaries, spermatheca, fat body.

INTRODUCTION

With the development of botany, agriculture and horticulture pollination was acknowledged to be the greatest benefit from the work of bees. The role of pollinators is performed not only by honey bees (*Apis mellifera*), by far the most widespread and the most efficient of pollinators, but also by many other insect species. Among those pollinators are also those which are referred to as wild bees. Of these, bumble bees (*Bombus*) were put on the top of the list of the most efficient pollinators. The ability to pollinate the so-called heterotropic flowers that have a peculiar morphology of calices and deeply hidden nectaries is explained by anatomical properties of bumble bees and especially by their tongues which are much longer than those of honey bees (6.4 in three-banded white-tailed bumble bee to 12.4 in white-tailed bumble bee. Bumble bees are the best pollinators of economically important plants such as red clover, clover crimson, alfalfa and hairy vetch (Dylewska et al 1970; Bawolski et al 1974; Anasiewicz and Warakomska 1977, Ruszkowski 1969a and 1969b). The seed yields of red clover in Poland are dependent in 71% on the pollination by bumble bees

(Biliński 1974). In addition, bumble bees show the ability to forage at low temperatures ca. +5°C (Corbet et al.1993) and at low light intensity (Heemert et al 1990). They frequently make their foraging flights even during rainy and windy weather.

The importance of bees increases with the development of vegetable growing and with increasingly more vegetable crops being grown under cover. This is because bumble bees will adapt better than honey bees to the difficult conditions of restricted space. As opposed to honey bees, they have no ability to inform one another about forage source and that makes them look for forage in the close vicinity of the nest. Owing to that bumble bees do not attempt to get outside the greenhouse or the plastic tunnel where other sources of food may be available. Owing to the pollination by bumble bees higher yields and a better quality fruits are obtained. With the benefits of bumble bees in plant pollination having been noticed as early as the beginning of the 20th century, attempts were made to rear those insects. Many rearing methods were developed, of which the laboratory method is the most efficient and the most widely used now. Denmark, the Netherlands and Belgium are now the bumble bee rearing giants with huge companies dealing in the production and trade of those insects. In many research centers worldwide research is being continued on improvements to bumble bee raising methods. In laboratory rearing the phenomenon of the failure of queens to go into diapause was observed. According to Biliński (unpublished data) the number of non-diapausing females may reach as many as 40 - 45%. Likewise, Wójtowski and Wilkaniec (1969) based on many years of rearing experience confirmed the existence of that phenomenon. Young queens that fail to diapause are bound to die. Diapause is a necessary element to keep them alive. The diapause of young inseminated bumble bee queens occurs at the beginning of the spring. Wójtowski and Wilkaniec (1969) suggest that the phenomenon is caused, among others, by the deficiency of fatty substances in the body or insufficient insemination of queens by the drones which, in turn, may be caused the underdevelopment of the reproductive organs.

In Denmark, filling of spermathecae in *Bombus terrestris* queens Latr. was studied (Schousboe 1994). The results of a three-year study showed that 3% of the naturally overwintered queens caught in the spring do not carry sperms in their spermathecae at all. Thus it can be assumed that the failure of the queens to get inseminated is the cause of the absence of diapause and so it is necessary to continue research into that problem.

The failure of young bumble bee queens to experience diapause drastically reduces the efficiency of bumble bee rearing. A lack of relevant literature data was the reason to undertake investigations into that problem.

The primary objective of this study was to analyze the causes of the failure of bumble bee queens to go into diapause.

Based on earlier suggestions by some investigators it was assumed that the causes behind the failure of young bumble bee queens to to into diapause may be the following:

— underdevelopment of reproductive organs
— insufficient filling of the spermatheca
— differences in the amount and the composition of the fat body

MATERIAL

The study was performed in the years 1995 - 2000. Diapausing and non--diapausing queens of the buff-tailed bumble bee (*Bombus terrestris* L.) raised in the laboratory and naturally overwintered queens caught in the wild in the spring were

Table 1

Bumble bee queens experimentally analyzed over the consecutive years

Year	Diapause bumble bee queens	Non-diapause bumble bee queens	Naturally overwintered queens
1997	37	37	-
1998	27	34	-
1999	28	18	-
2000*	-	-	40
Total	92	89	40

* queens hatched in 1999, naturally diapausing, caught in the spring of 2000

analyzed. The latter group of queens was introduced for study in 2000 as a reference. The species *B. terrestris* was chosen for study as the most frequently used in laboratory rearing and the most widespread experimental species. A total of 221 bumble bee queens were screened. Their number structure is shown in Table 1.

All bumble bee queens were examined for the size of their ovaries and spermathecae using the Microsscan-Lucia microscope imaging software. The number of sperms in spermathecae was determined in the Fuchs-Rosenthal chamber by taking counts of sperms in the physiological liquid solution. The weighing method was used to calculate the dry matter of the fat body.

The data for all the parameters were compared among the individual groups of bumble bee queens.

METHODS

Size of bumble bee female ovaries

The development of ovaries in diapausing and non-diapausing females was assessed by measuring ovary length and width. Microscan-Lucia microscope imaging software and a stereo microscope with an attached Mitsubishi CCD 100 camera were used.

Anasthetized bumble bee queens were pinned to a beeswax plate with an enthomological pin and the abdomen was cut open from the dorsal side. Next the intestine was removed to expose the ovaries and the whole reproductive system. The monitor image was saved and then measured.

A distance from the terminal filament to the mid-section of the oviduct was the measure of ovary length and the widest dilatation of the ovary tubes measured perpendicularly to their length was taken for ovary width. First the left and then the right ovary were measured. The ovaries were not dissected out of the abdomen but measured in their natural anatomical position. The magnification of 0.63 x12.5 was used for the measurements.

Analysis of the spermathecae of bumble bee queens

For greater accuracy, spermathecae were dissected, placed in a drop of physiological liquid and then their circumference and diameter at 2.5 x 12,5 magnification were measured using the same technique as that described for ovary measurements. Their volumes were calculated by substituting the measurement values in the formula for the volume of a sphere $v = {}^{4}/_{3}\Pi r^{3}$, with calculations of the volume of honey bee queen spermathecae taken as a model (Chuda-Mickiewicz 1998). Subsequently, the spermatheca was placed on a watch glass, cut open while mixing its content vigorously with 200 ml of Hyes liquid. The drop was placed in Fuchs-Rosenthal chamber and the sperms were counted at 20 x 10 magnification in ten large squares equivalent to 2 μl of the liquid using a phase contrast microscope. Finally, the number of sperms in the spermatheca was calculated.

Fat body of bumble bee queens

Dry matter of the fat body was determined using the weighing method. A small quantity of fine sand was sprinkled onto the bottom of weighing bottles and a thin glass rod was put inside. The weighing bottles were dried for an hour at 105°C, weighed and put in an ecsiccator under calcium chloride to evacuate moisture. Fat bodies lining the inside of abdomen rings were successively dissected from bumble bee queens and put in the weighing bottles and the bottles were re-weighed. A single fat body was put in each bottle. The fat body was ground with sand using the glass rod, dried at 105°C, taken out and re-weighed after being kept in an ecsiccator for 20 minutes. For each bumble bee queen fat body weight was calculated as the difference of the two weight measurements.

Statistical analysis

The comparison of the anatomical and physico-chemical measurements of internal organs in diapausing vs. non-diapausing bumble bee queens was made by using t-tests of the means. The statistics was performed using the Statgraphis Plus version 4.1 software. Naturally overwintered bumble bee queens were analysed in one year only and the results were not analysed statistically. In that case the means were used solely to make tentative comparisons with the data from other tested groups.

RESULTS

Ovary size in bumble bee queens

Ovary length

Because of the manner in which the measurements of ovary length and width were made and then recorded by the computer software the data for the left and for the right ovary were analyzed separately.

The values were subjected to T-test to find statistical differences between the means under comparison. In diapausing queens the mean length of the left ovary was highly significantly different from that in non-diapausing queens.

The values for the right ovary followed a similar pattern. The mean length of the right ovary was greater in diapausing than in non-diapausing queens. The T-test values showed a highly significant difference between the means (Table 2).

Table 2

Comparison of the left vs. the right ovary length in bumble bee queens (mm)

Queen group	Left ovary length	Right ovary length
Diapausing	min = 5,362	min =6,066
	max = 15,931	max =14,537
	$\bar{x}$ = 10,842	$\bar{x}$ = 10,992
Non-diapausing	min = 5,219	min =5,058
	max =14,461	max =19,562
	$\bar{x}$ = 9,461	$\bar{x}$ = 9,690
	$t_{emp.(p = 0.000054)} = 4,13 > t_{tab.(\alpha = 0.01)} = 2,60$	$t_{emp.(p = 0.00033)} = 3,65 > t_{tab.(\alpha = 0.01)} = 2,60$

Ovary width

The mean width of the left ovary in diapausing bumble bee queens was smaller than that in non-diapausing queens. However, when tested with the T-test the differences were found to be insignificant. Likewise, the width of the right ovary in diapausing queens was smaller than that in non-diapausing queens. Again, the differences were found to be insignificant. Table 3 shows the ranges and means for the width of the right and of the left ovary.

As a final stage of the study, a group of naturally overwintered and diapaused queens caught in the spring after was introduced for comparison in 2000. The results indicate that naturally diapaused bumble bee queens had ovaries that were close in size to those in laboratory-reared queens although the means for naturally diapaused queens were slightly higher than those for the remaining bumble queen groups (Table 4).

Spermathecae of bumble bee queens

The measurements of the spermathecae showed that all the groups of bumble bee queens had a similar spermatheca volume, which averaged from 0.0070 μl in naturally overwintered queens to 0.0072 μl in non-diapause queens to 0.0073 μl in reared queens that had experienced diapause. The means for diapause vs. non-diapause queens did not differ significantly (Table 5).

With regard to spermatheca filling with sperms the analyzed groups did differ from one another with the results averaging from 33089 for non diapause queens to 54140 for diapause queens to 67080 for naturally overwintered queens. A comparison for the filling of the spermatheca with sperms in diapause vs. non-diapause queens shows the existence of a significant difference between the means (Table 6).

Table 3

Comparison of the left vs. the right ovary width in bumble bee queens (mm)

Queen group	Left ovary width	Right ovary width
Diapausing	min = 0,496	min = 0,593
	max = 2,087	max = 2,121
	$\bar{x}$ = 1,0135	$\bar{x}$ = 1,054
Non-diapausing	min = 0,467	min = 0,495
	max = 2,257	max = 2,121
	$\bar{x}$ = 1,0705	$\bar{x}$ = 1,100
	$t_{emp.(p = 0.2231)}$ = = 1,22 > $t_{tab.(\alpha = 0.05)}$ = 1,97	$t_{emp.(p = 0.2743)}$ = = 1,09 > $t_{tab.(\alpha = 0.05)}$ = 1,97

Table 4

Ovary size in naturally overwintered queens (mm)

Left ovary length	Right ovary length	Left ovary width	Right overy width
min. = 8,461	min. = 9,305	min. = 0,794	min. = 0,786
max = 16,399	max = 17,008	max = 1,692	max = 1,64
$\bar{x}$ = 12,781	$\bar{x}$ = 12,582	$\bar{x}$ = 1,1699	$\bar{x}$ = 1,238

Table 5

Spermatheca volume in bumble bee queens

Queen group	Spermatheca volume (μl)
Diapause queens	min = 0,0024 max = 0,0139 $\bar{x}$ = 0,0073
Non-diapause queens	min = 0,0008 max = 0,0315 $\bar{x}$ = 0,0072
$t_{emp.(p = 0.98)} = 0,02 < t_{tab.(\alpha = 0.05)} = 1,97$	
Naturally overwintered queens	min = 0,0039 max = 0,0106 $\bar{x}$ = 0,0070

Table 6

Filling of spermatheca in diapause vs. non-diapause queens (number of sperms)

Queen group	Number of sperms in spermatheca
Diapause queens	min = 19900 max = 99200 $\bar{x}$ = 54140
Non-diapause queens	min = 2200 max = 90200 $\bar{x}$ = 33089
$t_{emp.(p = 2,131)} = 8,44 > t_{tab.(\alpha = 0.01)} = 2,60$	
Naturally overwintered queens	min = 40600 max = 85300 $\bar{x}$ = 67080

Fat body dry weight in bumble bee queens

Reared diapause queens were the highest in fat body averaging 0.0213 i.e. double the amount in non-diapause queens, the latter averaging 0.0158. The difference was statistically significant.

Naturally overwintered queens caught in the wild were substantially lower for fat body weight averaging 0.0068 g (Table 7).

DISCUSSION

No reports on ovary length and width and hence on ovary size in bumble bee queens have been found among available reference literature. The number of ovarioles in bumble bee queens is four in either ovary which is confirmed by Richard-Kenneth (1994) who in his paper compared the ovaries of bumble bees and .*Psithyrus*. The measurements of ovary length reported in this study showed that laboratory-raised queens experiencing diapause had ovaries that were significantly longer than those of non-diapause queens. That characteristic can be taken as an indicator of ovary development as it does not change during the female's lifetime. So ovary length can be treated as an indicator of the preparedness of bumble bee queens

Table 7

Fat body dry weight in bumble bee queens

Queen group	Fat body dry weight (g)
Diapause queens	min = 0,0022 max = 0,0926 $\bar{x}$ = 0,0213
Non-diapause queens	min = 0,0024 max = 0,0564 $\bar{x}$ = 0,0158
$t_{emp.(p = 0,0440)} = 2,035 > t_{tab.(\alpha = 0.05)} = 1,97$	
Naturally overwintered queens	min = 0,0018 max = 0,0120 $\bar{x}$ = 0,0068

to go into diapause and to undertake reproductive functions the following spring.

Ovary width varies over different periods of the female's life so that the characteristic can be taken as indicative of the insect's physiological development. Actually, since the bumble bee queens were analyzed over a fairly short time the values should not have varied much from one another. The widening of ovary tubes occurs only in the spring after the queens have fed intensively and started to lay eggs. Hence the markedly higher values of ovary width in naturally overwintered females in the spring of 2000.

The spermatheca volume in bumble bee queens averages from 0.0070 µl to 0.0073 µl in different queen groups. It looks like that value is fairly constant within the species. It is testified by the statistical analysis which demonstrated the absence of significant differences between the diapause and the non-diapause queens for spermatheca volume.

The average number of sperms per spermatheca was 54140 in diapause queens, 67080 in naturally overwintered queens and 33089 in non-diapause queens. Contrary to the data reported by Schousboe (1994) who investigated filling of spermathecae in artificially reared and naturally-raised queens, no empty spermatheca was found in any of the queens. The results obtained by the above-mentioned investigator in the years 1985 - 1987 revealed the existence of as many as 10% of spring bumble bee queens the spermathecae of which were empty. Tasei and Aupinel (1994) estimated the filling of spermathecae in reared bumble bee queens at 5800 to 36200 sperms. A slightly higher figure was obtained by Röseler (1973) in both spring and autumn queens. The investigator also examined bumble bee queens for the correlation of the number of sperms per spermatheca against the size of colony established by them and against the number of copulation events. However, he failed to demonstrate the correlation between those characteristics in *Bombus terrestris*. On the other hand, Sagakami (1976) did demonstrate the relationship between the number of sperms in the spermathecae of diapause bumble bee queens and colony size in several bumble bee species. In this author's previous study that covered only two years of experiments the average number of sperms per spermatheca was higher than that in this study and was 84950 for diapause queens and 38500 for non-diapause queens (Maciejewska 1998). Given the data from the author's investigations as well as literature reports it can be conjectured that the number of sperms per spermatheca of bumble bee queen is very variable and depends on many factors. The statistically significant difference in the average number of sperms per spermatheca between the queens that have experienced diapause and the non-diapause queens may be the reason behind the failure of the latter to go into diapause.

The fat body in insects originates from the cells of mesodermal sacs. In the majority of insects, including bumble bees, it forms two separate layers: a parietal layer that is adjacent to the body walls and an intestinal layer that surrounds the intestine and also other organs inside the body (Klimaszewski 1996). So it is an elastic mass supporting the internal organs. However, its main function, especially of its parietal layer is to accumulate storage nutritional substances to be utilized during the various development stages. A massive growth of the fat body is characteristic of insects which experience diapause during their development. Therefore, in the author's own studies the fat body lining the abdomen rings of bumble bee queens was sampled for analysis. The increase in the size of the fat body before the diapause is always preceded by intensive feeding which allows maximum accumulation of strorage food in the body. As early as in the first days of their life, young bumble bee queens store substantial amounts of food as the fat body, mainly in the abdomen (Dylewska 1966). During diapause, nearly all the food reserves become depleted. So the reserves in the fat body must be large enough to last through the winter.

The author's own study showed that the bumble bee queens that had experienced diapause had substantially more fat body than the non-diapause queens. So the quantity of fat body may be a factor that makes the adult insects ready to go into diapause and to survive that difficult period.

Pelt-Verkuil (1979) argues that the role of fat body in insects, especially during diapause, is not yet well understood. The fat body in *Hymenoptera* was investigated by, among others, Writz (1973) who also argues that, in spite of the wealth of literature concerning fat body, the data on this organ in *Hymenoptera* are still insufficient and fragmentary. Thus the study in that field are but a contribution making the way to further research on the role and the changes of the fat body in diapausing insects.

CONCLUSIONS

1. Of the anatomical characteristics of the reproductive organs of bumble bee queens that may have a significant effect on their diapause one should mention ovary length and filling of the spermatheca, or the number of sperms therein. The average values of the above characteristics were significantly higher in diapausing queens than in non-diapausing queens.
2. Both the higher average length of both ovaries and the higher number of sperms per spermatheca in queens raised in the wild and caught in the spring after having undergone diapause as compared to laboratory-reared queens may point to inadequate understanding of the needs of artificially reared bumble bee colonies.
3. Ovary width and spermatheca volume do not influence diapause in bumble bee queens since no significant differences were found between the mean values of those characteristics in diapause and non-diapause queens.
4. Fat body is one of the characteristics that govern diapausing vs. non-diapausing in bumble bee queens. Diapause queens were characterized by a statistically higher weight of fat body so they were better prepared to survive the diapause than non-diapause queens.

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PRZYCZYNY BRAKU DIAPAUZY U SAMIC TRZMIELI (*Bombus Latr.*, *Apoidea*)

Fliszkiewicz M.

Streszczenie

Badania przeprowadzono w latach 1995-2000 w Katedrze Hodowli Owadów Użytkowych w AR w Poznaniu. Ogółem przeanalizowano 221matek trzmielich z gatunku *Bombus terrestris*. Należały do nich matki zapadające i niezapadające w stan diapauzy pochodzące z hodowli zamkniętej, jak również grupa matek naturalnie przezimowanych pochodzących z odłowu.

Porównywano długość i szerokość jajników, objętość i wypełnienie zbiorniczka nasiennego oraz suchą masę ciała tłuszczowego.

Średnie wartości długości jajników oraz wypełnienia zbiorniczków nasiennych były statystycznie wysoce istotnie większe u matek diapauzujących w porównaniu z matkami niediapauzującymi. Można więc przyjąć, iż cechy te mają wpływ na zapadanie matek trzmielich w stan diapauzy. Natomiast wyższa średnia tych cech u matek z rodzin rozwijających się w warunkach naturalnych w porównaniu z matkami z hodowli laboratoryjnej mogą świadczyć o niepełnej znajomości potrzeb rodzin trzmielich rozwijających się w warunkach hodowli.

Szerokość jajników i objętość zbiorniczka nasiennego nie mają wpływu na przechodzenie samic trzmieli w stan diapauzy, ponieważ nie stwierdzono statystycznie istotnych różnic pomiędzy średnimi wartościami tych cech u matek, które zapadły w stan diapauzy, a matkami niediapauzującymi.

Wielkość ciała tłuszczowego decyduje o zapadaniu, bądź niezapadaniu matek trzmielich w stan diapauzy. Matki diapauzujące charakteryzowały się statystycznie istotnie większą suchą masą ciała tłuszczowego, a więc były lepiej przygotowane do przetrwania okresu diapauzy aniżeli matki, które nie zapadły w stan diapauzy.

Słowa kluczowe: Trzmiele, diapauza, jajniki, zbiorniczek nasienny, ciało tłuszczowe.