POLLEN HOARDING EFFECTIVENESS AND STRATEGIES
AS AFFECTED BY WORKER BEE GENOTYPE
II. GENETIC DIVERSITY WITHIN A COLONY

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Summary

Pollen harvesting effectiveness and strategy in mixed nucleus colonies made up of two
different worker bee groups (50% each) and in homogeneous colonies each containing worker
bees of only one group were compared. Three experiments were run, each with the two different
groups of worker bees. The colony genotype on the amount of harvested pollen and on the
choice of pollen source was discernible. In mixed colonies the pollen yield was most of the time
higher than that in homogeneous colonies. It can be conjectured that the workers of the two
different groups made up for each other’s pollen gathering abilities, which is additionally
confirmed by the analysis of the choice of pollen source that they made.

Keywords: pollen, pollen foragers, genetic diversity, Apis mellifera.

INTRODUCTION

The majority of productivity-related traits of the bee colony is the outcome of
the collective effort of genetically diverse
worker bees. Their cooperation in foraging
for pollen and for nectar as a genetic and
evolutionary consequence of polyandry
(Koeniger 1986) being an example of ad-
aptation through diversity rather than
through adaptation to a niche (Mackay
1981, Paleolog and Maciejowski 1990)
attracted the interest of socio-biologists.
The study of the effects of such cooperation
contribute to the understanding of evolution
and of the functioning of the super-body of
the colony of social insects viewed from the
standpoint of colony selection (Robinson
and Page 1989, Fewell and Winston
1996). Those problems are also of interest
from the standpoint of evaluation of the
productive value of honeybee queens
(based on the efficiency of daughter worker
bees) as mixing of different groups of bees
in one colony being the result of apiary
management practices (replacement of
brood frames, colony strengthening, change
in colony structure due to raids) or the result
of bee drifting (Taber 1988) may distort
the results of such an evaluation. Thus both
from the standpoint of the evolution theory
and from that of practical beekeeping (se-
lection for high pollen output colonies) it is
worthwhile to get a more in-depth understand-
ing of the effect of worker bee cooper-
ation, more particularly so, if two
generically different large groups of bees
will be artificially mixed in one colony. It is
worthwhile to check if the efficiency of
such a mixed colony will be intermediate or
if it will surpass the efficiency of either
component worker group. Those things
considered, we have decided to compare
pollen collecting efficiency and preferred
sources of pollen in honeybee colonies both
homogeneous or made up of genetically di-
verse workers.
METHODS
The study was run in the apiary of the Agricultural University, Lublin, Poland, where the bees foraged on the vegetation of arable fields, idle lands, parks and municipal greenery areas. Three successive experiments were on the following dates: from June 8 to June 12 and from July 11 to July 13. Altogether, worker bees from four genetically different groups were used (Table 1a). In each experiment only two of those groups were included. They were used to settle three nucleus colonies (simple “colony” referred to further in the text) in the following manner: From each of the groups (strong colonies) three litres of worker bees of a complete age structure were collected. In each of the experiments each colony was made up of two litres of bees, two of them being homogeneous and containing 100% of bees of one group only and the third colony being made of 50% of one group of 50% of the other (Table 1b). The colonies were introduced in Langstroth hives with three combs and a virgin queen. All queens were siblings. There were small pollen stores in two combs with trace amounts of bee bread and several dozen brood cells in the third. In the course of the experiments the emerging brood was removed to preserve the genetic structure of worker bees within a colony. Each hive was provided with a pollen trap. The pollen from the traps was collected on the daily basis, weighed and, subsequently, the average weight of a single pollen load was estimated and the pollen loads were segregated according to colour. The percentages of pollen loads of each colour (each species) and the average weights of one pollen load of a given species (colour) were calculated. The plants of origin were also identified (Warakomska 1962).

RESULTS AND DISCUSSION
The effect of the genotype of worker bee on the amount of harvested pollen was easily discernible (Table 2). Interestingly, in

Table 1a
Four genetic groups of bees used in experiments 1, 2 and 3

<table>
<thead>
<tr>
<th>Native*, from north-eastern Poland (MM1)</th>
<th>Caucasian hybrid (CU)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native *, from south-eastern Poland (MM2)</td>
<td>Italian hybrid (IT)</td>
</tr>
</tbody>
</table>

* - contain *Apis mellifera mellifera* component;
( ) - group designations referred to further in the text and in the tables are given in parentheses

Table 1b
Groups of worker bees making up an experiment nucleus colonies in each of the three experiments

<table>
<thead>
<tr>
<th>Colony 1 (homogeneous)</th>
<th>Experiment 1</th>
<th>Experiment 2</th>
<th>Experiment 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100% MM1</td>
<td>100% MM2</td>
<td>100% MM1</td>
</tr>
<tr>
<td>Colony 2 (homogeneous)</td>
<td>100% IT</td>
<td>100% CU</td>
<td>100% CU</td>
</tr>
<tr>
<td>Colony 3 (mixed)</td>
<td>50% MM1+50% IT</td>
<td>50% MM2+50% CU</td>
<td>50% MM1+50% CU</td>
</tr>
</tbody>
</table>

For designations see Table 1
Table 2

Average weights of pollen loads trapped during 1 day and average weights of a single pollen load in mixed vs. homogeneous colonies in three successive experiments

<table>
<thead>
<tr>
<th>Colony</th>
<th>Homogeneous</th>
<th>Mixed</th>
<th>Homogeneous</th>
<th>Mixed</th>
<th>Homogeneous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. 1</td>
<td>Bees</td>
<td>MM1</td>
<td>MM1/IT</td>
<td>IT</td>
<td>MM1</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>3.92a</td>
<td>3.95a</td>
<td>2.93Aa</td>
<td>9.1a</td>
</tr>
<tr>
<td></td>
<td>Bees</td>
<td>MM2</td>
<td>MM2/CU</td>
<td>CU</td>
<td>MM2</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>3.46A</td>
<td>9.41B</td>
<td>2.54A</td>
<td>8.0A</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>Bees</td>
<td>MM1</td>
<td>MM1/CU</td>
<td>CU</td>
<td>MM1</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>0.36B</td>
<td>0.79A</td>
<td>0.66A</td>
<td>5.9bc</td>
</tr>
</tbody>
</table>

Small letters - differences significant at P<0.05, capital letters - differences significant at P<0.01

Table 3

Percentage of pollen loads of different colour in samples collected from homogeneous and mixed colonies in three successive experiments

<table>
<thead>
<tr>
<th>Colony</th>
<th>Pollen load colour</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>green</td>
</tr>
<tr>
<td>Exp. 1</td>
<td>homogeneous (MM1)</td>
</tr>
<tr>
<td></td>
<td>mixed (MM1/IT)</td>
</tr>
<tr>
<td></td>
<td>homogeneous (IT)</td>
</tr>
<tr>
<td>Exp. 2</td>
<td>homogeneous (MM2)</td>
</tr>
<tr>
<td></td>
<td>mixed (MM2/CU)</td>
</tr>
<tr>
<td></td>
<td>homogeneous (CU)</td>
</tr>
<tr>
<td>Exp. 3</td>
<td>homogeneous (MM1)</td>
</tr>
<tr>
<td></td>
<td>mixed (MM1/CU)</td>
</tr>
<tr>
<td></td>
<td>homogeneous (CU)</td>
</tr>
</tbody>
</table>

χ² test: for P<0.01 χ²=21.66; Exp. 1 - χ²=93.0; Exp. 2 - χ²=97.9; Exp. 3 - χ²=53.4.
For explanations see Table 1

mixed colonies made up of more or less efficient pollen foragers the overall pollen harvest was higher (Experiment 2) or at least equal to that characteristic of the more efficient gatherers in the colony. It is worth adding that in mixed colonies pollen harvests were always the highest but from the standpoint of statistics in experiments 1 and 3 they did not depart from those characteristic of the more efficient foragers of the colonies. That tendency was, none-the-less, consistent and apparent. Thus it can be assumed that worker bees of two different genetic groups mixed in one colony
Table 4

<table>
<thead>
<tr>
<th>Pollen load colour</th>
<th>green</th>
<th>yellow</th>
<th>orange</th>
<th>creamy</th>
<th>brown</th>
<th>white</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. 1 Sinapis arvensis Type: Vicia</td>
<td>Type: Achillea</td>
<td>-</td>
<td>Eleagnus</td>
<td>Type: Anthriscus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. 2 Type: Rubus Type: Tilia</td>
<td>Althaea, Cucurbita</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exp. 3 - Plantago Type: Taraxacum</td>
<td>Cornus</td>
<td>Cornus, Trifolium repens</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5

<table>
<thead>
<tr>
<th>Colonies</th>
<th>Pollen load colour</th>
<th>green</th>
<th>yellow</th>
<th>orange</th>
<th>creamy</th>
<th>brown</th>
<th>white</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exp. 1 homogeneous (MM1)</td>
<td>8.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>mixed (MM1/IT)</td>
<td>8.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.7&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-</td>
<td>9.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>homogeneous (IT)</td>
<td>10.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>9.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Exp. 2 homogeneous (MM2)</td>
<td>-</td>
<td>10.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>mixed (MM2/CU)</td>
<td>8.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>homogeneous (CU)</td>
<td>9.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>9.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Exp. 3 homogeneous (MM1)</td>
<td>-</td>
<td>3.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.0</td>
<td>6.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>mixed (MM1/CU)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>homogeneous (CU)</td>
<td>-</td>
<td>3.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
<td>8.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

Small letters - differences significant at P<0.05

Compensated for one another’s abilities the source of their advantage being the diversity of the mixed colony (Robinson and Page 1989, Fewell and Page 1993). However, it is an open question whether it was a mere compensation or an additional quality that had arisen as a result of an interaction (similar to heterosis). The superiority of the mixed colonies over the homogeneous ones might point to such a solution and to further indicate that, in spite of the high heritability of pollen efficiency (Page and Fondrk 1995) an admixture of alien bees may grossly distort the results of the evaluation of the genetic value of a queen. Compared to the colonies CU and IT the colonies MM1 and MM2 did not gather less pollen but they foraged fewer plants (Table 3). Any of all four bee groups tested in experiments 1, 2 and 3 preferred different pollen species (Tables 3 and 4) but in mixed colonies the pollen was gathered from the plants that were foraged by the bees of both constituent groups. When confronted with the results shown in Table 1 reported by Percival (1955) those observations might
confirm the mutual compensatory effect of the worker bees thereby increasing the potential of a mixed colony.

In experiments 2 and 3 the weight of a single pollen load (Table 3) in mixed colonies was higher than that in homogeneous colonies, especially in experiment 2 where the difference was statistically significant. It is worth reminding that it is also the amount of gathered pollen that was the greatest in that experiment. In the case of a larger weight of a single pollen load it is the positive correlation between the amount of gathered pollen and the weight of a single pollen load rather than the cooperation between worker bees that is of relevance. This point of view was confirmed in another studies (Grabowski et al. 2000, Paleolog et al. 2003). No consistent effect of colony type on the weight of a single pollen load over different pollen donors was recorded. It can only be remarked that, depending on the source of pollen, the pollen loads were of different size and the pollen loads gathered in experiment 3 (July) were substantially smaller. It was in agreement with our earlier observations and with the suggestions by other investigators according to whom the weight of a pollen load is primarily related to environmental factors and to the pollen donor species (Lipiński 1982).

REFERENCES


Taber S. (1988) - Drifting, Glean. in bee cult., 6, 398-399.

EFEKTYWNOŚĆ I STRATEGIA ZBIERANIA PYŁKU W ZALEŻNOŚCI OD GENOTYPÓW ROBOTNIC
II. GENETYCZNA RÓŻNORODNOŚĆ WEWNĄTRZ RODZINY

P a l e o l o g  J., B o r s u k  G., O l s z e w s k i  K.

S t r e s z c z e n i e

Porównano efektywność i strategię zbierania pyłu w rodzinkach jednorodnych złożonych tylko z jednej grupy robotnic i w rodzinkach mieszanych składających się z dwu różnych grup robotnic (po 50%), - tych samych, które wchodziły w skład rodzinek jednorodnych. Przeprowadzono 3 kolejne doświadczenia z różnymi grupami pszczół (tabela 1a i 1b). Wpływ genotypu robotnic na ilość przyniesionego przez nie pyłu i na wybór jego źródeł był widoczny a pszczoly miejscowe nie odbiegały od importowanych (tabela 2). W rodzinkach mieszanych, zbiór pyłu był najczęściej wyższy niż w rodzinach jednorodnych. Można przypuszczać, że robotnice dwu różnych grup genetycznych, wymieszanych w jednej rodzinie, wzajemnie uzupełniały swoje możliwości lub nawet potęgowały efektywność swego działania poprzez interakcję. Pogląd ten potwierdza analiza różnorodności wybieranych źródeł pozyskiwanego pyłu, gdyż rodziny mieszane wykorzystywały źródła preferowane przez pszczoly z obu tworzących je grup (tabela 3, 5). Większe zbiory pyłu często pociągały za sobą wzrost masy obróży, choć cecha ta bardziej zależała od gatunku rośliny i środowiska.

Słowa kluczowe: pyłek, zbieranie pyłu, genetyczna różnorodność, Apis mellifera.