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Behavioural characteristics of honey bee (*Apis mellifera*) colonies containing mix of workers of divergent behavioural traits

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Defence behaviour (sting test), hygienic behaviour (needle test) and syrup foraging rate were studied in honey bee (*Apis mellifera*) colonies artificially made up of defensive and gentle bees (1:1), and were compared with homogenous colonies made up only of either defensive or gentle bees. The defensive bees turned out to be high-hygienic whereas the gentle bees were low-hygienic. The mixed colonies were defensive in terms of time to the first sting, but gentle or intermediate in terms of the number of stings. Colonies of mixed high-hygienic (defensive) and low-hygienic (gentle) bees were found to be intermediate or high-hygienic when they were monitored after a period of 12 or 24 h, respectively. Foraging rate was also markedly differentiated in homogenous colonies. The colonies with a mixture of good and poor foragers exhibited a poor foraging rate. Repeatability of the monitored traits was higher in the 100% defensive/high-hygienic colonies (higher genetic effect) than in 100% gentle/low-hygienic colonies. Efficient workers performed tasks by themselves and did not solicit help from non-efficient workers. Results of combining of different bee types occurred different. Interworker interactions were mostly non-additive for foraging and defensive behaviour, but additive for hygienic behaviour.

KEY WORDS: *Apis mellifera* / defensive behaviour / foraging rate / honey bee / hygienic behaviour/ worker interactions / mixed colonies

A honey bee (*Apis mellifera*) colony is composed of worker groups of different genotypes [Koeniger 1986] and behaviours [Breed and Page 1989, Fewell and Page 1993]. The genotypic diversity within the colony is artificially increased when

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beekeepers move brood frames to different hives or join colonies together. It is also increased by bee drifting [Taber 1988]. The question arises of how do these different worker groups affect one another? Some studies have shown that the behaviour of an individual worker can be altered by the specific within-colony environment created by other workers [Paxton *et al*. 1994] and that the behaviour of one worker group can modify the behaviour of another [Trump *et al*. 1967, Spivak and Gillam 1993]. Most economic features result from the behaviour of the whole colony and the specific genotypic mix of workers can affect the estimated colony value due to interworker interactions [Guzman-Novoa and Page 1994]. If measurements of a mixed colony behavioural characteristics are the additive composites of diverse worker groups, then the expected colony value should be the mean from these groups. However, if interactions between particular worker groups are non-additive, the mixed colony value should markedly differ from that mean. In the present study, the defensive response of the colonies artificially made up of a mixture of worker bees (1:1) that originated from defensive or from gentle source colonies was compared with the defence of homogenous colonies that consisted of either only bees from the gentle or only from the defensive source colonies. In addition, hygienic behaviour and foraging rate of these colonies were studied since both traits have been reported to be correlated (or not) with a colony defence [Winston 1995, Kefuss *et al.*, 1996]. In this study the impact exerted by various physical worker mixes on the whole colony value/behaviour was investigated, and the respective contribution studied of each worker group.

Material and methods

Eight different source colonies of *Apis mellifera* were used to found experimental nucleus-colonies. They included four defensive colonies: Native *Apis mellifera* from the conservation population (MM), Carniolan × native hybrids (F2C), two colonies of the unknown origin acquired from local beekeepers (UN1, UN2) and four gentle colonies from the pure commercial stocks: Carniolan (CR), Caucasian (CU), Buckfast (BC) and Buckfast × Italian (BI) hybrid bees. The first sting came 2-10 s after a colony disturbing in the defensive, while after 47-78 s in the gentle source colonies.

Six different comparisons were made using the same following procedure given below. Selected were two out of eight source colonies, one defensive and the other gentle. After sunset, three kg worker bees were shaken into an empty box, half from the brood nest and half from the upper super, in each of the two selected colonies. In this way, two groups of three kg of workers of balanced age structure were obtained and used to create three nucleus-colonies (colonies 1, 2 and 3), each of them consisting of two kg of bees (Tab. 1). Colonies 1 and 2 were homogenous and each of them consisted of bees taken from only one of the two source colonies, whereas colony 3 was the mix of bees from both source colonies (gentle:defensive = 1:1). The colonies were hived in Langstroth hives containing four frames (one open brood, one honey store, two empty) and were headed by young egg-laying queens, all sisters,

representing a genotypic type differing from that of the tested bees. Thus, the queen effects were minimized [Paxton *et al*. 1994, Lipiński 2007]. Such nucleus colonies of almost identical strength and structure were created as a colony strength affects the results of stinging, foraging and hygienic behaviour. Subsequently, the colonies were transported to a new location and positioned in such a way as to minimize bee drifting. Twenty-four h later the stinging and the needle tests commenced simultaneously in these colonies. Next, the foraging test was performed. During each test capped brood was removed before bee emergence in order to maintain the initial structure of the colonies.

The sting test was carried out as follows. An oval, brown coloured target (360 cm^2), made of sheepskin, was waved in front the hive entrance of each assayed colony after the bees had been disturbed by intensive knocking on the hive. The time at which the first sting was given to the target (TFS) and the number of stings received within two min past the first sting (SN) were recorded. During 15 consecutive days, 15 repetitions of the test were carried out in the case of comparisons 1, 2, 5 and 6, and 20 in the case of comparisons 3 and 4. In comparisons 3, 5 and 6, a film record of mixed colony bees attacking the target was made. F2C, UN1 and UN2 defensive bees were significantly darker in body colour than BC and BI gentle bees, which were light. In this way dark-coloured defensive and light-coloured gentle workers were distinguished and then counted on the film once every 15 s during a period of 2 min measured from the moment the first sting had been given.

Simultaneously with the stinging tests, 10 repetitions of the needle test were performed in the same colonies in which the stinging tests were done. In each repetition, a section of comb (100 cells) containing pierced capped brood was placed in the centre of each brood nest. Hygienic behaviour was quantified as the percentage of cells uncapped (UC) and as the percentage of dead brood removed (BR), both after 12 and 24 h.

The foraging test was performed upon the completion of the stinging and hygienic behaviour assays, but only in comparisons 1, 2, 5 and 6 because only within each of these comparisons the strength of the assayed nucleus colonies was still similar. A group of 0.7 kg young, nest bees of an appropriate worker mixture (see Tab. 1) was introduced into each colony before the beginning of the foraging test in order to maintain the colony age structure. Each colony was then placed individually into a flight cage (3 x 2 x 2 m) and supplied with sugar : water (1:1) syrup from an artificial feeding station placed within the cage, 1.5 m away from the hive entrance. The syrup level was monitored over the following seven days.

The one-way ANOVA (SAS), including multiple range tests, was performed separately for each of the six comparisons to verify the colony-type effects. The repeatability coefficient (REML, VARCOMP, SAS) was also estimated, for mixed and homogenous nuclei-colonies separately, by partitioning of the phenotypic variation into intracolony (test repetitions; V_E) and intercolony variation. The coefficient informs about the upper limits to the ratio V_G/V_P (upper limits to h^2). Furthermore,

Table 1. Composition of nucleus colonies of worker bees (*Apis mellifera*) assayed

Compa-rison (C)	Colony 1 homogenous defensive	Colony 2 homogenous gentle	Colony 3 mixed
1	2 kg MM	2 kg BC	1 kg MM + 1 kg BC (MM/BC)
2	2 kg MM	2 kg CU	1 kg MM + 1 kg CU (MM/CU)
3	2 kg F2C	2 kg BC	1 kg F2C + 1 kg BC (F2C/BC)
4	2 kg F2C	2 kg CR	1 kg F2C + 1 kg CR (F2C/CR)
5	2 kg UN1	2 kg BI	1 kg UN1 + 1 kg BI (UN1/BI)
6	2 kg UN2	2 kg BI	1 kg UN2 + 1 kg BI (UN2/BI)

MM – *Apis mellifera mellifera*; F2C – Carniolan crossbreds; UN1, UN2 – bees of unknown origin; BC – Buckfast; CU – Caucasian; CR – Carniolan; BI – Buckfast × Italian. Symbols used in this table are further applied in the text.

the correlation coefficients (for the dependent values – repetitions) between some of the examined traits and the linear regression for the consecutive repetitions within each colony, separately for TFS, SN, BR, and UC, were estimated. To estimate the interworker interaction the following approach was applied: When two different groups of workers maintained in homogenous colonies and characterized by a low and a high value of a given trait were mixed in the proportion of 1:1, then the value of that trait in such a mixed colony should be lower than that observed in the better homogenous colony by about 50% of the difference between the trait values in the good and in the poor homogenous colony (PV-GV). Only in such a case, the additive interaction between these two groups of workers could take place (if measurements of a mixed colony trait are the additive components of diverse worker groups, then the expected colony value should be the mean from these groups). Consequently, if only the trait value in this mixed colony is not lower than that observed in the better homogenous colony by about 50%, the interworker non-additive interaction occurs.

Results and discussion

Mean time to the first sting (TFS) was almost identical in the defensive homogenous and in the mixed colonies, in which the admixture of 50% of gentle bees decreased TFS by only 3, 11, 5 and 0 per cent points (pcp) of PV-GV. This was, however, observed only in comparisons 2, 3, 4 and 5 (Tab. 2). In comparisons 1 and 6, the 50% admixture of gentle bees decreased TFS in the mixed colonies, but only by 25 and 27 pcp of PV-GV, respectively. The SN values (number of stings given within 2 min after the first sting) in the mixed colonies were even more similar to those in the gentle homogenous colonies in comparisons 1, 2, 3 and 6 (higher only by 30, 20, 27 and 21 pcp of PV-GV, respectively), whereas in comparisons 4 and 6, the values were similar to the means for the gentle and defensive colonies. So, the mixed colonies were defensive in terms of TFS, but gentle or intermediate in terms of SN.

Table 2. Results of the sting test

Comparison (C)	Colony	TFS		SN	
		mean	SD	mean	SD
1	MM	2.7^{A}	0.3	94.8^{A}	4.2
	MM/BC	8.0^{B}	0.7	33.1^{B}	3.4
	BC	24.2^{C}	2.5	6.5^{C}	0.8
2	MM	3.3^{A}	0.3	111.3^{A}	21.7
	MM/CU	4.4^{A}	0.4	26.4^{B}	5.1
	CU	36.2^{B}	5.9	5.2^{B}	1.1
3	F2C	6.4^{A}	0.4	83.6^{A}	3.4
	F2C/BC	10.6^{A}	0.9	27.1^{B}	3.0
	BC	45.1^{B}	3.1	6.6^{C}	0.5
4	F2C	4.1^{A}	0.5	92.7^{A}	8.4
	F2C/CR	5.6^{A}	1.1	50.4^{B}	5.2
	CR	37.4^{B}	3.1	4.9^{C}	0.6
5	UN1	9.8^{A}	2.1	129.8^{A}	18.1
	UN1/BI	8.6^{A}	1.5	$71.\ 8^{B}$	14.1
	BI	40.1^{B}	6.5	22.1^{C}	3.1
6	UN2	14.5^{a}	3.5	67.8^{A}	13.1
	UN2/BI	26.8^{b}	6.8	37.3^{B}	9.6
	BI	61.2^{C}	10.1	29.0^{B}	8.2
Total	defensive	6.9^{A}	1.7	96.7^{A}	11.7
	mixed	10.7^{A}	2.1	41.1^{B}	6.9
	gentle	40.7^{B}	5.8	12.4^{C}	2.6

TFS – mean time to first sting; SN – mean number of stings; MM – *Apis mellifera mellifera*; F2C – Carniolan crossbreds; UN1, UN2 – bees of unknown origin; BC – Buckfast; CU – Caucasian; CR – Carniolan; BI – Buckfast × Italian.
$^{aA,\cdots}$Means bearing different superscripts differ significantly at: small letters – P≤0,05; capitals – P≤0,01.
Each trait within each comparison (C) was compared separately.

High contribution of the defensive bees to the mixed colony defense can suggest the behavioural dominance of these bees [Guzman-Novoa and Page 1994, Page and Robinson 1991] which, however, in this study, was observed only in the case of TFS. "Time to respond to alarm pheromone" and the "number of stings" are controlled by different genes [Collins *et al*. 1980, 1988] which corresponds to the negative correlation between TFS and SN shown in the present report (-0.63, P<0.001) as well as by Guzman-Novoa and Page [1994], and also could result in different types of the interworker interactions regarding TFS and SN as observed in this study. The results presented here also revealed that the mixed colony defense could be unpredictable as it was affected by the type of the mixed workers. Stort [1974], Guzman-Novoa and Page [1994] and Paxton *et al*. [1994] also indicated that the worker interactions depended on the specific genotypic mix of workers.

The film analysis revealed that in the initial phase of the test (Tab. 3), individual defenders attacked the target mostly alone. Later on, more of the gentle bees were

stimulated to attack, but the defensive bees still "did the majority of the job", which was particularly in evidence in comparisons 3 and 5. The defenders' out-flying rate (alert) in the mixed colonies was similar to that observed in the homogenous defensive colonies. In the mixed colonies, however, more of the attacking workers were hitting the target without stinging it and the ratio of defenders that were stinging the target straight away was higher in the homogenous defensive colonies. This finding might also explain different types of interworker interactions in the case of SN and TFS. Could the within-colony environment (pheromones?) of the mixed colony stimulate them only to the out-fly response (alert), but not to the mass stinging?

Table 3. Number of defensive bees attacking the leather target (in per cent of the total number of attacking bees (defensive + gentle) counted on the film at 15 s intervals in the mixed colonies

Comparison (C)	n	Intervals measured from the moment the first sting was made							
		15 s	30 s	45 s	60 s	75 s	90 s	105 s	120 s
3	20	91*	84*	79*	83*	75*	69*	72*	68
5	15	98*	91*	85*	74*	81*	72*	65	61
6	15	69*	67*	59	65*	49	43	51	55

(*) - The observed percentage differs significantly (chi-square; $P<0.05$) from that expected (50).
n – sample size.

Table 4. The repeatability coefficients for the characteristics assessed

Colonies	TFS	SN	After 12 h		After 24 h	
			BR	UC	BR	UC
Homogenous (+)	0.48	0.35	0.55	0.64	0.86	0.72
Mixed	0.34	0.21	0.40	0.22	0.69	0.33
Homogenous (–)	0.24	0.19	0.28	0.19	0.33	0.18

(+) – defensive/more-hygienic colonies; (-) – gentle-hygienic colonies; TFS – time to the first sting; SN – number of stings;. UC – percentage of uncapped cells; BR – percentage of dead brood removed.
REML was performed separately for "homogenous colonies (+)", "homogenous colonies (-)" and for "mixed colonies".

The colony type affected variation in neither TFS nor SN, and therefore no means or ANOVA results are presented here. The repeatability coefficient of TFS and SN was higher in the defensive than in the gentle colonies and it was intermediate in the mixed colonies (Tab. 4). This result suggests that TFS and SN were more dependent on the colony mean genotype in the defensive colonies, whereas in the gentle colonies, they were probably influenced to a greater extent by the environment. Page and Robinson [1991] and Guzman-Novoa and Page [1994] indicated that the violent defensive

response is determined by a few major genes, and therefore, the defensive bees are characterized by a markedly low threshold of response to environmental stimuli. Consequently, their defensive response could be less dependent upon environmental changes. On the other hand, visible variation of TFS and SN observed both within the defensive and within the gentle colonies in the present study as compared to the Kastberger *et al*. [2004] findings, suggest that some other additive minor genes could determine the colony's defensive ability in the European bees.

Results shown in Figure 1 compared to those presented in Table 2 revealed that the homogenous defensive colonies were at the same time high-hygienic whereas the gentle homogenous colonies were low-hygienic. So, the colonies being the mixture of the defensive and the gentle bees were also the mixture of the high-hygienic and low-hygienic bees. The fact that hygienic bees were at the same time defensive was indicated also by Winston [1995], while Kefuss *et al*. [1996] did not observe such a correlation and pointed out that Rothenbuhler had already demonstrated the lack of a link between stinging and hygienic behaviour. The different nature of such a link could probably be a result of the fact that divergent types of bees were mixed by different authors.

The results of needle tests are presented in Figure 1. When percentage of the uncapped cells (UC) was monitored after 12 h (in Fig. 1 the colony symbols marked with stars) no significant differences between the colony types were identified. When UC was monitored after 24 h (colony symbols without stars), the intercolony differences were visible and showed almost the same pattern as that observed in the case of percentage of the dead brood removed cells (BR).

BR monitored after 12 h approximated the mean values in the mixed colonies in comparisons 1, 2, 3 and 6. In comparisons 4 and 5 however, BR was only slightly higher than that observed in the homogenous low-hygienic (gentle) colonies and it has been estimated that these differences amounted only to 14 and 27 pcp of PV-GV (difference in the trait values between good and poor homogenous colony), respectively. After 24 h, however, BR in the mixed colonies was similar to that observed in the homogenous defensive colonies (high-hygienic) in comparisons 1, 2, 3 and 5, but it was higher, respectively, by only 32 and 17 pcp of PV-GV than that observed in the homogenous gentle (low-hygienic) colonies, in comparisons 4 and 6. Concluding, colonies with mixed 50% poor and 50% good cleaners mostly showed the intermediate BR when monitored after 12 h. After 24h, however, BR was rather similar to that observed in the colonies consisting of 100% good cleaners, except for comparisons 4 and 6. Trump *et al*. [1967] observed a high dead-brood removal rate in colonies containing 50% hygienic bees. Spivak and Gillam [1993] showed that an addition of 30% of hygienic bees to the non-hygienic colonies did not increase the hygienic behaviour, whereas an addition of 30% of non-hygienic bees to hygienic colonies suppressed this behaviour. Palacio *et al*. [2000] concluded that if it was possible to obtain a colony with some hygienic workers in it, the whole colony would behave hygienically. The results presented in this report might suggest, that

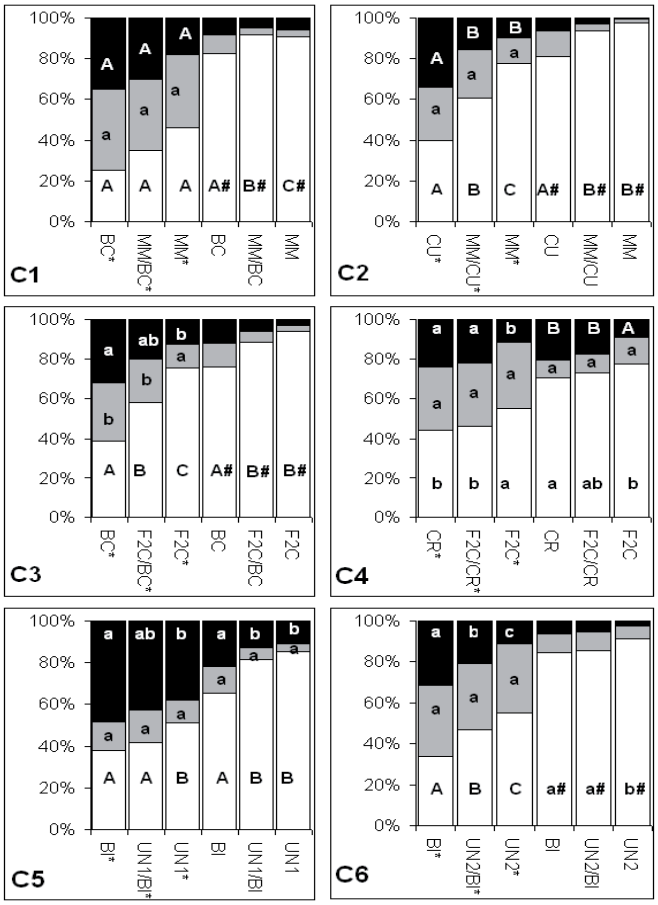

Fig. 1. Percentages of dead brood cells removed (white), uncapped cells (grey) and cells that were not cleaned out at all (black) in all colonies measured after 12 and 24 h. **MM** – *Apis mellifera mellifera*; **F2C** – Carniolan crossbreeds; **UN1**, **UN2** – bees of the unknown origin; **BC** – Buckfast; **CU** – Caucasian; **CR** – Carniolan; **BI** – Buckfast x Italian. **C1**, **C2**, **C3**, **C4**, **C5** and **C6** – comparisons 1, 2, 3, 4, 5 and 6. Asterisks put at the colony symbols stand for the results obtained when colonies were monitored after 12 hours. Lack of asterisks at the same colony symbols stands for the results obtained when the same colonies were monitored after 24 hours. Colony means were compared separately within each trait (for black, grey and white parts of the columns) and within each of the two measurements (after 12 and 24 hours – colony symbols with and without asterisks, respectively). So, the comparisons were performed for each characteristic nested in each measurement separately. Means bearing different superscripts are significantly different at: capitals – $P<0.01$ and small letters – $P<0.05$. **(#)** – results of the statistical comparison were the same for all the three examined characteristics (for black, grey, white part of a column). Therefore, for simplification, the letters are marked only at the white parts of columns. The BR acronym is being used in the text instead of the "percentage of dead brood removed cells" (white part of the column in Fig. 1) and the UC acronym instead of the "percentage of uncapped cells" (grey part of a column in Fig. 1).

during the first 12 h of the test, 100% of good cleaners in homogenous colonies were be able to do more work than only 50% of the good cleaners in the mixed colonies. After 24 h, however, because of the longer period of time allowed for the cleaning process, 50% of the good cleaners in the mixed colonies were able to do the same work as 100% of the good cleaners in the homogenous colonies. If this was indeed the case, the more hygienic bees were not able to stimulate the less hygienic ones to the effective cleaning. This study also revealed that the hygienic behaviour could depend not only on the percentage of hygienic workers within the mixed colony, but also on the genotypes of the mixed workers. It was interesting that particular type of worker combination markedly influenced BR (uncapping + cleaning) but did not affect the UC (uncapping only) – Figure 1.

The coefficients of correlation between UC and BR amounted to -0.80 ($P<0.01$) and -0.84 ($P<0.001$), for results obtained after 12 h and 24 h, respectively. Palacio *et al*. [2000] concluded that UC and BR are determined by different genes, what corresponds with negative correlation shown. The repeatability coefficients of UC and BR were markedly higher in the homogenous more-hygienic than in the homogenous less-hygienic colonies (Tab. 4). In the mixed colonies, it ranged between the values observed in the homogenous colonies. It seems that UC and BR were more dependent on the colony mean genotypes in the high-hygienic than in the low-hygienic colonies, where they depended mostly upon the environment. Spivak and Downey [1998] also reported that high-hygienic colonies demonstrated a more consistent rate of brood removal between consecutive trials, whereas the brood removal rate in the non-hygienic colonies varied and depended mostly upon within-colony environment. No systematic trends were found for variation of UC and BR. Neither increase nor decrease in BR, UC, TFS and SN values was also observed over the consecutive repetitions of the tests because the linear regression coefficients for the consecutive repetitions within each colony and each trait were not found significant. Therefore, the respective results are not presented here. It seems, however, that multiple repetitions of the sting/needle tests result neither in decrease/increase of the thresholds of the defensive response (adaptation to the stimulus) nor in bees getting more practice in cell cleaning. These results are not in accordance with the findings of Free [1988], who reported that honey bees could adapt to alarm pheromone over consecutive trials. Results of this study also suggested that similarly to foragers [Breed and Page 1989, Fewell and Page 1993, Paleolog *et al*. 2003], more efficient cleaners/defenders tend to do their work on their own taking up an appropriate task dependently on an individual worker's decision. However, a specific worker mix could influence the threshold of the response.

Contrary to Winston [1995], the present experiment showed no visible relation between defensiveness and foraging rate as the syrup intake was not always higher in the defensive/high-hygienic and lower in the gentle/low-hygienic colonies. The correlation coefficients among the foraging rate and TFS, SN, UC and BR were additionally estimated and significant relationships were not found. Therefore, the

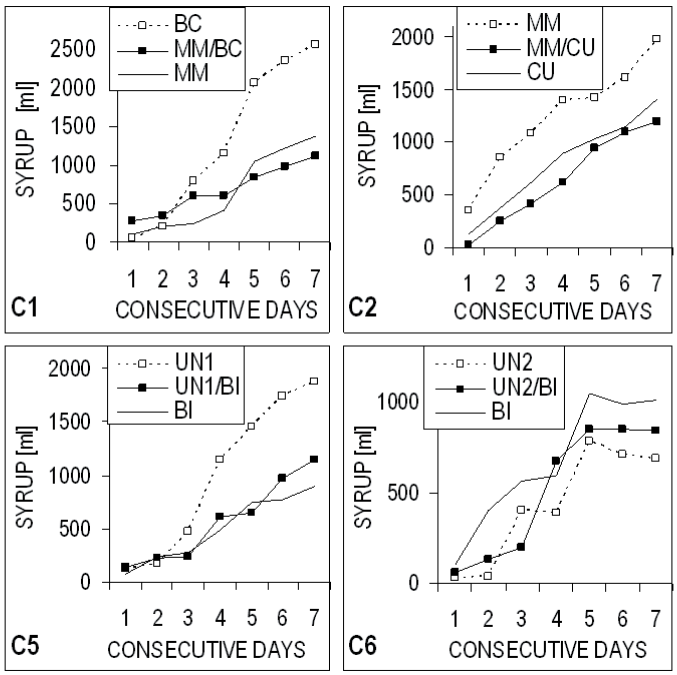

Fig. 2. The volume of sugar syrup collected by homogenous and combined colonies in flight cages. MM – *Apis mellifera mellifera*; UN1, UN2 – bees of the unknown origin; **BC** – Buckfast; CU – Caucasian; BI – Buckfast x Italian. C1, C2, C5 and C6 – comparisons 1, 2, 5 and 6.

results are not presented here. Nevertheless, in the homogenous defensive/high-hygienic colonies the foraging rate (Fig. 2) was markedly different from that in homogenous gentle/low-hygienic colonies in comparisons 1, 2 and 5. So, worker interactions could be studied. It is hard to explain, however, why the colonies which were a mixture of workers and showed showing high or low foraging rate (1:1) consumed even less syrup than those composed of 100% non-efficient foragers. Thom *et al*. [2000] found that a colony adjusted its foraging effort by changing the number of foragers. Therefore, in that case, some more complicated, non-additive interactions might occur. It is also possible that some other factors, e.g.interworker communication, were involved.

It is particularly interesting that in this experiment the interworker genotypic interactions were mostly non-additive with regard to foraging and defensive behaviour, *i.e*. when older "flying" workers were involved. In the case of hygienic behaviour, *i.e*. concerning young nest bees, these interactions were mostly additive.

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Zachowanie pszczoły miodnej *(Apis mellifera)* w rodzinach utworzonych sztucznie z robotnic o zróżnicowanych cechach behawioralnych

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

Badano zachowania obronne (test żądłowy), behawior higieniczny (test igłowy) i tempo zbierania syropu w sztucznie utworzonych rodzinach pszczoły miodnej (*Apis mellifera*) zawierających mieszaninę (1:1) robotnic agresywnych i łagodnych. Wyniki porównano z zachowaniami robotnic z rodzin jednorodnych, złożonych wyłącznie z pszczół łagodnych, bądź wyłącznie z pszczół agresywnych. Pszczoły agresywne okazały się wysoce higieniczne, a pszczoły łagodne – nisko higieniczne. Rodziny mieszane były agresywne pod względem czasu upływającego od podrażnienia do pozostawienia pierwszego żądła, ale pośrednie lub łagodne pod względem liczby wbitych w cel żądeł. Rodziny mieszane składające się z pszczół wysoce higienicznych (agresywnych) i nisko higienicznych (łagodnych) okazały się pośrednie albo wysoce higieniczne gdy obserwowano je odpowiednio po 12 albo 24 godzinach. Rodziny jednorodne różniły się także tempem zbierania syropu. Rodziny mieszane złożone z dobrych i złych zbieraczek zbierały syrop bardzo słabo. Powtarzalność analizowanych cech była wyższa w rodzinach jednorodnych agresywnych/wysoce higienicznych (silniejsze uwarunkowania genetyczne) niż w rodzinach łagodnych/nisko higienicznych. Wydajne robotnice wykonywały pracę samodzielnie, nie mobilizując do niej robotnic mniej wydajnych. Wyniki mieszania różnych typów pszczół były różne. Interakcje między robotnicami były w większości nieaddytywne dla zachowań obronnych i zbierania syropu. W przypadku zachowań higienicznych interakcje te były addytywne.