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Biting behaviour as a tactic of escape in two bumblebee species with different nesting habits, Bombus terrestris L. and B. pascuorum Scopoli (Hymenoptera: Apidae)

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Abstract. Workers of two bumblebee species, Bombus terrestris L. and B. pascuorum Scopoli, had to find the way of escape out of a test tube closed with a paper membrane stretched against its open end. Nearly all of the tested individuals solved successfully that task by tearing a hole in the membrane closing the tube. However, their escape behaviour showed significant interspecific differences. B. terrestris started biting the membrane sooner than B. pascuorum, and they were biting it more persistently. These behavioural differences matched well the differences in the nesting ecology of these two species. Whereas B. pascuorum is a surface-nesting species, B. terrestris nest in underground cavities connected with the outside world by long tunnels. B. terrestris are thus more likely to be well adapted to deal with obstacles obstructing their way, and/or to have more experience in removing them. Neither the efficiency of biting behaviour as a tactic of escape, nor the total test time differed significantly between the tested species.

Short communication

Key words: escape, tactic, bumblebees, Bombus, Bombus terrestris, Bombus pascuorum, Apidae

In Hymenoptera, vigorous and persistent escape behaviour may be triggered in response to a wide range of situations, ranging from exposure to repellent odours (Hoagland 1931; Vowles 1964, 1965) to submersion in water (Morgan 1981) and to confinement (Hess 1913; Bertholf 1931; Godzińska 1983, 1988). Like the majority of important functions, escape behaviour of these insects involves, as a rule, more than a single tactic. On one hand, Hymenoptera often respond to escape situations by displaying photopositive behaviour (Hess 1913; Bertholf 1931; Morgan 1981; Godzińska 1983, 1988). Photopositivity is fairly reliable as a tactic of escape, because, as a rule, light signalizes open space. However, Hymenoptera may also respond to escape situations, and, in particular, to confinement, by attempts to remove obstacles obstructing their way. Such behaviour was described already by Verlaine (1925) in his study of maze learning in social wasps Paravespula germanica L. Initially, that author used a maze made of cardboard, but, instead of learning it, the wasps kept biting holes in its walls, so that finally he had to exchange his apparatus for a glass one.

In a more recent experiment, Godzińska (1988) compared the behaviour of workers of two species of bumblebees, Bombus terrestris L. and B. pascuorum Scopoli, during their attempts to escape out of a test tube plugged with soil. Although that task was solved relatively easily by nearly all of the tested individuals of both species, all the parametres chosen to characterize their behaviour showed significant interspecific differences. The performance of B. terrestris was closer to optimality than the performance of B. pascuorum in all examined respects: B. terrestris started to dig sooner, they were digging more persistently, their digging was more efficient, and they needed less time to escape out of the tube than B. pascuorum.

These differences in the escape behaviour of B. terrestris and B. pascuorum matched well the differences in their nesting ecology. Whereas B. pascuorum is a surface-nesting species, B. terrestris nest mostly in abandoned rodent nests, or in other underground cavities connected with the outside world by long tunnels (Alford 1975). The ability to clear away the soil obstructing a narrow passage in a quick and efficient way is undoubtedly far more important for the survival of colonies of underground-nesting bumblebees. Better escape performance of B. terrestris in tubes plugged with soil might thus have resulted ultimately from some preprogrammed factor(s) which had evolved as an adaptation to underground nesting. On the other hand, however, as all the workers tested in the discussed study were taken from among wild living foragers visiting plants, B. terrestris might have performed better than B. pascuorum simply because they had already some experience in removing soil, having acquired it in their nest tunnels prior to the test. Finally, both these groups of factors (preprogrammed and acquired) might have contributed to the interspecific differences observed in the discussed study. The question of causal factors underlying the observed phenomena remained thus unanswered.

Another so far unresolved question was whether the differences in the escape performance of B. terrestris and B. pascuorum exist solely on the level of specific readiness to perform digging behaviour, or, perhaps, also on the level of the readiness to perform other activities belonging to the system of behavioural subroutines underlying the escape behaviour of these insects.

In order to throw more light on these questions, in the present study workers of B. terrestris and B. pascuorum were tested in a modified experimental situation. This time, the bees were confined in a test tube closed with a thin paper membrane stretched against its open end. To escape, they had to bite in it a hole sufficiently large to be able to crawl out.

The tests were carried out in the field, at several sites near Mrozy and Krześlin in Siedlce District in "central-eastern" Poland during August and early September 1984. We used as subjects wild living workers of Bombus pascuorum Scopoli and B. terrestris L., taken from among foragers visiting various wild and cultivated plants, mostly Melampyrum nemorosum L., Galeopsis tetrahit L., and Trifolium pratense L. They were captured using a small glass beaker (10 cm long and 3 cm in diameter. Immediately after the capture, each bee was transferred into a test tube, 15 cm long and 1.5 cm in diameter. The tube was then closed with a thin double-layered paper membrane, stretched against its open end, and then pushed inside by means of a tightly fitting cylindrical piston, made of a smaller glass tube open at both ends. Such a way of fixing the membrane made sure that the tested bee remained in the full view of the observer during the whole test.

During the test, the tube was kept in a horizontal position, and its closed, transparent end was kept oriented in the direction of sunlight. The two sides of the tube were screened by means of two perpendicular side screens of white cardboard, each 20 cm long and 3 cm high.

The tests were performed on sunny days only, at the air temperature of 22±2°C. To avoid possible heat exhaustion of the tested bees, the tubes were not exposed directly to sun radiation, but shadowed from above. As demonstrated in preliminary tests (Godzińska 1988), such a simple precaution is very efficient in preventing overheating of the tested bees. Humidity conditions in the tubes were fairly constant: as a rule, relative humidity of the air reached 100% soon after the start of each test, as demonstrated by the condensation of vapour on the inside walls of the tube.

Each test continued either until the escape of the bee through the torn membrane, or, in few cases in which the bee became inactive, during at least ten minutes from its last recorded movement. At the end of each test the bee was recaptured, marked with paint to avoid its testing for the second time, and released free.

During the test, the observer noted all successive behavioural events, with the accuracy up to one second. In the present study, we will, however, report only the data concerning biting behaviour directed at the paper membrane closing the tube.

On the basis of these data, the following indices were calculated:

1. t = the latency from the start of the test to the onset of the initial biting bout (i.e. to the first biting movement during which the mandibles of the bee touched the membrane closing the tube) (s);
2. d = the duration of the initial biting bout d (s);
3. N = the number of biting bouts per test;
4. B = the total time spent biting and tearing the paper during the test (s);
5. T = the total test time (the latency from the start of the test to the final escape of the bee out of the tube) T (s).

Altogether, 103 workers of B. terrestris and 60 workers of B. pascuorum were tested. The complete record of the successive behavioural events was obtained for 90 workers of B. terrestris and 40 workers of B. pascuorum. However, the actual sample sizes for each of the investigated parametres were, as a rule, larger (see Table I), as the data from the otherwise incomplete records were also taken into account.

The distributions of the values of t, d, N, B, and T obtained for B. terrestris and B. pascuorum were compared by means of the two-tailed Mann-Whitney U test.

The results of the study showed that all tested individuals responded to confinement in a test tube closed with a paper membrane by vigorous escape behaviour. In all cases, their attempts to escape out of that tube involved, among others, biting behaviour directed at the membrane closing their way out. In the majority of the cases (97.1% of B. terrestris and 91.7% of B. pascuorum) biting behaviour led eventually to the escape of the tested bee out of the tube. However, 3 workers of B. terrestris (2.9%) and 5 workers of B. pascuorum (9.2%) failed to solve that task: they gradually ceased to show escape behaviour, and then they became wholly inactive. As already mentioned, to be included into that category, the bee had to stop its attempts at escape and to keep totally and uninterruptedly motionless during at least ten minutes. The ratio of the individuals which have solved the escape task to those which failed to solve it and became inactive did not differ significantly between the tested species ($\aleph^2_{11}$: NS).

All of the parametres chosen to characterize the behaviour of the tested bees showed high intraspecific variability (Table I). Significant interspecific differences were also found in the case of three of these indices, namely, (1) t (the latency to the onset of biting, characterizing the initial readiness of the bee to employ biting behaviour as a tactic of escape), (2) d (the duration of the initial biting bout, characterizing the initial persistence of the bee in maintaining biting activity), and (3) N (the number of biting bouts during the test, characterizing the overall persistence of the bee in biting the paper membrane) (Table I). In all these cases, the behaviour of B. terrestris was closer to optimality than the behaviour of B. pascuorum: B. terrestris started to bite the membrane earlier than B. pascuorum, their initial biting bouts were of longer duration, and they performed less biting bouts during the test (in other words, they made fewer interruptions of biting during the test) (Table I).

The ranges of the values of the indices t, d and N obtained for B. terrestris and B. pascuorum largely overlapped. In particular, the minimum values of these three indices were nearly identical in both tested species. In the case of index N, also the maximum values obtained for B. terrestris and B. pascuorum were very close (Table I).

The values of the index B (the total time spent biting the membrane during the test), characterizing the efficiency of biting behaviour, did not differ significantly between B. terrestris and B. pascuorum. In particular, the median values of that index were nearly identical in both these species. However, in B. terrestris the index B took values within a wider range than in B. pascuorum (Table I).

TABLE I

Intra-specific variability and inter-specific differences in the values of the indices characterizing biting behaviour of workers of B. terrestris and B. pascuorum. *n*, sample size; R, range (the minimum and the maximum value of the index); M, median

Index		B. terrestris			B. pascuorum			*P*
		n	R	M	*n*	R	M	
t (latency to the initial biting bout)	(s)	92	1-455	35.0	47	2-605	45.0	*
d (duration of the initial biting bout)	(s)	98	1-290	13.5	43	1-135	9.0	*
N (number of biting bouts per test)		91	1-37	6.4	43	2-34	11.3	*
B (total time spent biting during the test)	(s)	100	73-1143	302.5	40	81-925	301.0	NS
T (total test time)	(s)	99	147-3554	581.0	55	162-2337	718.0	NS

*, $P<0.05$ (two-tailed Mann-Whitney U test)

The values of the T index (the total test time) also did not differ between the tested species. However, a non-significant trend towards the superiority of B. terrestris over B. pascuorum was again observed here: B. terrestris tended to escape out of the test tubes sooner than B. pascuorum. Similarly as index B, also the index T took values within a wider range in B. terrestris than in B. pascuorum (Table I).

The present report belongs to a very small group of studies dealing with the spontaneous escape behaviour of Hymenoptera (Morgan 1981, Godzińska 1983, 1988). So far, the occurrence of biting behaviour in response to confinement was reported in Hymenoptera only by Verlaine (1925) in the wasps Paravespula germanica L. trained in a cardboard maze, and by Godzińska (1988) in the bumblebees Bombus pascuorum Scopoli kept in test tubes closed with plugs of filter paper. However, as far as we know, our present report provides the first experimental analysis of biting behaviour employed as a tactic of escape by Hymenoptera.

Escape behaviour displayed by B. terrestris and B.pascuorum in response to confinement in a test tube was investigated by Godzińska (1988) in the study mentioned already in the Introduction. Similarly as in that study, also in our present experiment escape performance was closer to optimality in the case of B. terrestris than in the case of B. pascuorum. B. terrestris started biting the paper membrane earlier, and they were more persistent in employing that escape tactic than B. pascuorum. Significant interspecific differences in the persistence in biting were present from the beginning of the test: already the initial biting bouts were significantly longer in B. terrestris than in B. pascuorum.

We can thus conclude that at least some of the interspecific differences in the escape behaviour of B. terrestris and B. pascuorum cannot be reduced to the differences in the specific readiness to perform digging behaviour.

Interspecific differences discovered in the present study were, however, less important than in the previous experiment: they were all significant at the level of 0.05 only, whereas those discovered previously were all significant at the level of 0.001. Moreover, whereas in the previous study B. terrestris performed better than B. pascuorum with respect to all indices chosen to characterize their escape behaviour,in the present case neither the efficiency of biting behaviour (characterized by index B), nor the total test time (T) differed between B. terrestris and B. pascuorum.

The common absence of interspecific differences in the case of indices B and T suggests that in the present experiment it was the efficiency of biting which had the decisive importance for determining the total test time. That conclusion is supported additionnally by the fact that both B and T took values within a wider range in the case of B. terrestris than in the case of B. pascuorum. Factors which differed significantly between the tested species (the initial readiness to start biting, and the persistence in maintaining that activity uninterruptedly) played, evidently, only a relatively minor role in minimizing the time needed by the bees to escape. Their influence was not wholly absent: whereas the median values of B were practically identical in both tested species, the median value of T was, however, lower in B.terrestris than in B. pascuorum (Table I). Nevertheless, their effect was not sufficiently important to lead to significant interspecific differences in the total test time.

We should also like to stress that, in spite of significant differences between the values of t, d and N obtained for B. terrestris and B. pascuorum, the minimum values of these indices were nearly identical in both these species. In other words, the cases of escape performance close to optimality, with respect to either the latency to the beginning of biting, or the persistence in biting, occurred not only in B. terrestris, but also in B. pascuorum.

The relative importance of preprogrammed and acquired factors in controlling the escape behaviour of B. terrestris and B. pascuorum in a tube closed with a paper membrane cannot be, as yet, determined. It is very probable that the workers of B. terrestris used in our tests had already some experience in removing natural obstacles obstructing their nest tunnels (soil, small roots, etc.). We cannot exclude that they transferred their possible experience in removing such obstacles on the experimental situation created in our present tests. Strikingly, in the present study the performance of B. terrestris and B. pascuorum differed only with respect to the latency to the onset of biting, and to the persistence in biting. These differences do not necessarily reflect the differences on the level of specific readiness to perform biting behaviour; rather than that, they may reflect the differences in a more general readiness to display behaviour directed at dealing with any obstacle obstructing the way, encoded on a higher level of integration of the system of behavioural subroutines underlying the escape behaviour in the bumblebees. The possible previous experience of B. terrestris in dealing with natural obstructions of their nest tunnels might have led to some facilitation on that level, and these acquired modifications might have, in turn, led to better performance of these bees in a test tube closed with a paper membrane.

The contribution of acquired factors to interspecific differences discovered in our present study seems thus probable, but it cannot yet be considered as demonstrated. At the same time, the contribution of preprogrammed factors to these differences cannot be excluded anymore.

Preprogrammed factors may be responsible also for the similarities of some aspects of behaviour of B. terrestris and B. pascuorum observed in the present experimental situation. At the start of its adult life, each bumblebee has to gnaw its way through the top of its cocoon (Free and Butler, 1959). Similar efficiency of biting behaviour of B. terrestris and B. pascuorum may reflect preprogrammed adaptations to that behaviour, equally important for both tested species.

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