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SHORT COMMUNICATION

Pheromone-mediated attraction in burying beetles

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Introduction

In a recent paper Bartlett (1987) tried to obtain some evidence for a sex attractant in burying beetles. In laboratory and field experiments he found that male and female burying beetles are significantly more likely to go to a container with a mouse buried by a *Necrophorus* male than to one with a hand-buried mouse. From his experiments he deduced that males attract other beetles to the corpse. But it is not unlikely that hand-buried mice are less attractive for *Necrophorus* than mice buried by beetles. In a field study carried out by Wilson *et al.* (1984) mice buried by a pair of *Necrophorus* were frequently (more than 50%) taken over by other *Necrophorus* individuals the day after burial. These mice must have been attractive for *Necrophorus* though there was no luring male. So Bartlett's experiments may be influenced by the odour of the carcass buried by the males.

Pukowski (1933) was the first to report a conspicuous behaviour of *Necrophorus* males that have found a carcass on which no female is present. These males take a typical posture: the extended abdomen is pointing up, the head touching the ground, and from time to time the tip of the abdomen is moved slightly up and down in such a way that the intersegmental membranes can be seen. The term 'sterzeln' she used for this kind of behaviour is derived from apidology where it describes a similar posture taken by honey bee workers during the release of pheromones attractive to other workers.

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In this paper we show a set of very simple laboratory experiments which clearly show that 'sterzeling' males emit a volatile substance and that females are attracted to this substance. In a previous paper (Müller & Eggert, 1987) we showed that *Necrophorus* males attract individuals of their own and of congeneric species even in the absence of a carcass. Furthermore, we were able to demonstrate that under laboratory conditions all males show that 'sterzeln' behaviour as soon as they are sexually mature without having encountered a carcass (Eggert & Müller, 1988). So we are able to test the significance of the 'sterzeln' behaviour and its effects on female *Necrophorus* without the influence of the odour of carrion.

Methods

The tested individuals were F1 or F2 offspring from field-caught *Necrophorus vespilloides* Herbst (Coleoptera: Silphidae). They were separated according to sex after emergence from the pupae and kept at 20°C at a light–dark cycle of 16/8. They were regularly fed freshly killed meal-worms. 5 days before the onset of the experiments, they were individually put into small plastic containers with moist filter paper. The general construction of the experimental design is shown in Fig. 1. As a wind source, we used a simple ventilator placed 170 cm away from the centre of a peat-covered arena (diameter 62 cm) divided into sixteen sectors of equal size (22.5° per sector). The males used were placed 46 cm upwind and downwind, respectively, from the centre of the arena. A lamp was placed some 70 cm above the centre of the arena in order to

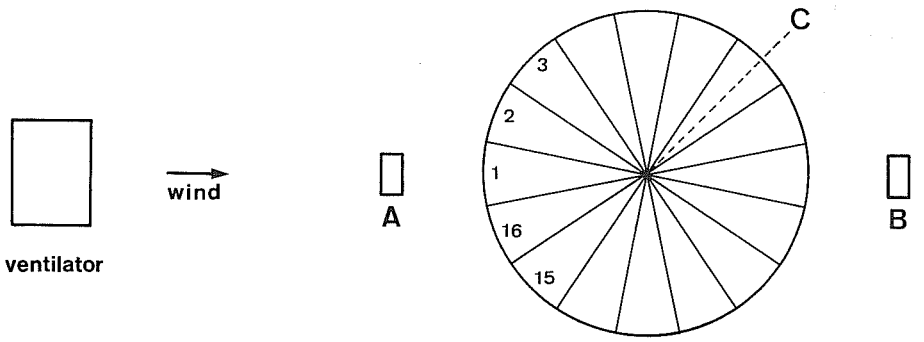

FIG. 1. Experimental design for orientation tests. A, B: position of container with male upwind (A) or downwind (B) of the female; C: centre of experimental arena = starting point for the female; distance between ventilator and arena not to true scale.

exclude the possibility of orientation to light. The females tested were transferred to the centre of the arena while sitting on the filter paper. If they had not shown any disturbance reactions (stridulation, hiding beneath the filter paper) during the next 10 s, the experiment started. The behaviour of the female was recorded during 180 s after a male had been introduced. When a female walked outside the experimental arena, the sector in which she left the arena was recorded. We termed a female's locomotion 'directed towards the male' if she left the arena in sector 1, 2 or 16. Females who flew off were not considered. The males were not removed from their containers in order not to disturb them. Instead, the upper half of the container was removed. Three different sets of experiments were carried out; their design is specified in the results.

Results

In the first experiment in which the 'sterzeling' males were placed upwind of the females (Table 1a), all of the tested females left the experimental arena within 180 s, and all but one left by sector 1, 2 or 16. In the second experiment (Table 1b) we first put a 'sterzeling' male downwind of the female for 3 min. During that time none out of thirty females showed any reaction. After that, we placed the same male upwind of the female. Then all females left the filter paper and walked out of the arena within the given time and all left by sector 1, 2 or 16. In the third experiment we tested each female with two different males (Table 1c). First we put a 'non-sterzeling' male upwind of the female after 3 min we replaced this male by a 'sterzeling' one. In the first part of this experiment only five

TABLE 1. Proportions of females reacting to males under different experimental conditions and direction of their locomotion.

Experimental conditions	Replicates (n)	Reacting p (% of n)	Left the arena in sector:		
			1	2 or 16	Other
(a) 'Sterzeling' male upwind	23	100%	17 (74%)	5 (22%)	1 (4%)
(b) 'Sterzeling' male downwind	30	0%			
'Sterzeling' male upwind	30	100%	20 (67%)	10 (33%)	0
(c) 'Non-sterzeling' male upwind	46	11%	0	0	5 (100%)
'Sterzeling' male upwind	46	100%	39 (85%)	7 (15%)	0

out of forty-six females walked away from the centre and left the arena; their motions were not directed towards the male. In the second part all females walked out of the arena and all left by sector 1, 2 or 16. Because in experiments 2 and 3 no female walked upwind in the absence of either an upwind male (experiment 2) or when the male was not 'sterzeling' (experiment 3), we did not test the reaction of females in the absence of males.

Discussion

The fact that male *Necrophorus* which are alone at a carcass show a typical behaviour named 'sterzeln' was published by Pukowski (1933). Three years later she published another paper in which she described two observations showing that female *Necrophorus* really are attracted by a 'sterzeling' male (Mosebach, 1936; Mosebach's maiden name is Pukowski). So Bartlett (1987) is incorrect in stating that 'Pukowski did not try to show directly that females were attracted by males'. From her observations Mosebach concluded that the attraction is due to the male's behaviour and she argued that it must be mediated by a volatile substance. Many investigators after Pukowski agreed with her interpretation. However, there are no investigations which clearly demonstrate that 'sterzeling' males attract females by means of pheromonal communication. The main problem of such an investigation is the influence of the carcass which – though buried – remains attractive for burying beetles (Wilson *et al.*, 1984). Because the 'sterzeln' behaviour is not dependent on the presence of carrion, we studied its effects on female behaviour using males that had not been supplied a carcass.

Our first experiment clearly shows that 'sterzeling' males are able to attract females. The second experiment gives clear evidence that the attraction is caused by a volatile substance and not by other cues such as visual or acoustical signals. The third experiment shows that males not showing the 'sterzeln' behaviour are not attractive for females.

Since males release pheromones and attract females even in the absence of a carcass (Müller & Eggert, 1987), the announcement of the presence of a carcass (Pukowski, 1933; Mosebach, 1936; Bartlett, 1987) cannot fully explain the biological significance of the 'sterzeln' behaviour.

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