

### Short communication

## Absence of chemical alarm in a primitively eusocial wasp (*Belonogaster petiolata*, Hymenoptera: Vespidae)

M. G. Keeping\*

Zoology Department, University of the Witwatersrand, Johannesburg, South Africa

*Key words:* *Belonogaster*, Polistinae, alarm pheromone, defense, venom.

### Summary

The hypothesis that *Belonogaster petiolata* (fam. Vespidae) is able to communicate alarm chemically, using odours released with the venom, was tested in bioassays involving presentation of artificial targets to a wasp colony, simultaneously with crushed venom apparatuses. The odour of venom did not lower the threshold of attack and visual stimuli alone (particularly a black, moving object) were sufficient to release attack. Venom odour on a previously stung target probably does not play a role in focusing further attacks on such a target. The results therefore support the null hypothesis that a venom-based alarm pheromone is absent in this species.

### Introduction

Compared with the ants and highly eusocial bees, little is known about chemical communication of alarm in the social wasps (Jeanne, in press). To date, there is evidence for alarm pheromones in the venom of five vespine species, two swarm-founding polistine species and three American species of the independent-founding genus *Polistes* (reviewed by Jeanne, in press; see also Kojima, 1994). The possible occurrence of alarm pheromones in an African independent-founding genus, *Belonogaster*, has not been investigated.

The present study tests the hypothesis that females of *B. petiolata* communicate alarm chemically, using odours present in the venom. When agitated females of this species were placed in a vial or held with forceps, a strong, acrid odour was produced; the same odour was detectable from crushed poison sacs and glands

---

\* Present address: Entomology Department, South African Sugar Association Experiment Station, Private Bag X02, Mt. Edgecombe 4300, South Africa

of freshly killed females, indicating venom as its source. Such a venom-based odourant, released on the nest or during stinging, may serve to recruit nestmates to a state of alarm and lower the attack threshold.

### Materials and methods

Bioassays were performed in mid-summer (January, 1988) when colonies of *B. petiolata* consist largely of workers and reproductive brood (Keeping, 1989). A colony containing 28 females (no males) was suspended beneath the eaves of a greenhouse on the campus of the University of the Witwatersrand. The nest was positioned ca. 10 cm from plastic fly screening over a window and 1.5 m above the ground. The system used to test the alarm response to venom odour, as well as the effects of colour and movement on attack behaviour, was almost identical to that used by Jeanne (1982) for *Polistes canadensis*. The wasps were allowed to attack four models with the following characteristics: dark, moving; dark, stationary; light, moving; light, stationary. Each model consisted of a 120 ml plastic bottle suspended from a 15 cm length of string, if it was moving, or a 15 cm length of stiff wire if it was stationary, and was wrapped in either black or white paper, presenting an area of 54 cm<sup>2</sup>. The models were suspended from a dowel framework to form a square, 30 cm on a side. The framework was lashed to a tripod and the latter was positioned with the model system ca. 50 cm from the nest and centred on it. The background for presentation of the models was a slope over-grown with small shrubs.

A large cardboard screen was suspended between the test apparatus and the nest between trials, to allow for the removal of the apparatus without disturbing the wasps. Trials were performed between 10 h and 16 h, when the colony was most active and responded well. Temperatures during the test period ranged between 27 and 30 °C. A gentle current of air was directed over the nest by means of a 30 cm fan placed inside the greenhouse and blowing through the screening opposite the nest. The nest was therefore upwind of the models, so that venom odour deposited on the models did not reach the nest.

For each test, the venom apparatus from a single wasp (inactivated on ice) was carefully removed and crushed on a 5.5 cm diameter filter paper disc. The filter paper, secured to the end of a dowel using a paper clip, was then moved slowly and steadily into a position one to three cm upwind of the nest. At the same time, the moving models were set in motion by means of a dowel operated through the greenhouse window. The plane of movement of the models was approximately perpendicular to the wasps' line of sight from the nest. The alarm response of the wasps was quantified by counting the number of direct attacks on the models, which produced a loud rap as the wasps hit the paper. The number of attacks or inspections of the filter paper disc was also noted. Each trial lasted until all attacks on the models had ceased (approximately 30 seconds).

For the controls, a clean filter paper disc was presented in the same way. Controls and tests ( $n=12$  replicates each) were paired and the order in which they were performed was alternated between trials. The positions of the models were randomized between trials. The paper of models which were attacked was changed so that

**Table 1.** Behavioural bioassays of alarm response of *B. petiolata* to venom odour. Data are the number of attacks on four visual models. Number of trials yielding a response is given in parentheses. The total number of attacks occurring during the controls was not significantly different from the number occurring during the presentation of venom sacs and sting apparatuses ( $\chi^2 = 0.02$ ; d.f. = 1;  $p > 0.90$ ;  $\chi^2$  tests)

	No. of trials	Models				Total
		Moving		Stationary		
		Dark	Light	Dark	Light	
Control	12 (6)	21	3	0	0	24
Test	12 (9)	10	9	1	3	23
Total		31	12	1	3	47

venom odour on the models did not influence attack behaviour. Trials were separated by 10 to 15 mins to minimize the effects of habitation.

## Results

Crushed venom sacs and sting apparatuses presented next to the nest produced no significant increase in the total number of attacks on the four visual models (Table 1), indicating that volatile substances in the venom were not capable of recruiting the wasps to a state of alarm and reducing their attack threshold. The wasps readily attacked the models in the absence of venom (Table 1). Only one "inspection" of the filter paper was recorded, in which an individual briefly hovered near the filter paper (with venom) without landing. Venom odour therefore does not appear to attract female *B. petiolata*, suggesting that targets which have been stung previously and carry venom deposits, are unlikely to be favoured targets for further attacks.

A significantly higher total number of attacks was directed at the dark, moving model, than at any other model (Table 1;  $\chi^2$  tests;  $p < 0.005$ ). The effects of colour and movement were, however, independent of one another ( $\chi^2 = 3.37$ ; d.f. = 1;  $\chi^2$  contingency table). With a background of heterogeneous vegetation, movement in the absence of colour is a stronger releaser of attack than is (dark) colour in the absence of movement (Table 1;  $\chi^2 = 9.31$ ;  $p < 0.005$ ;  $\chi^2$  contingency table).

## Discussion

The absence of any evident alarm role for venom odour in *B. petiolata* concurs with findings on several species in other vespidae genera. Freisling (1943) and Maschwitz (1964) failed to find evidence for chemical alarm in three European species of *Polistes*. Among the Vespinae, tests on three species from North America (including *Vespula vulgaris*) provided no evidence for the existence of any alarm substance (Hermann and Blum, 1981; Akre, 1982).

*B. petiolata* may represent a primitive stage in the evolution of venom-based alarm substances in the Polistinae; namely, a distinctive volatile odour is present in the venom and presumably released during stinging, but a behavioural response to it, either as a cue (odour deposited on target during stinging) or as a pheromone (odour released on nest independently of stinging), has not evolved. A test of this hypothesis clearly requires an extensive knowledge, presently lacking, of the occurrence and chemical nature of venom-based volatiles and alarm substances in the Polistinae.

### Acknowledgements

Greg Jones provided invaluable assistance in carrying out the bioassays. The manuscript benefited from criticisms by Robin Crewe, Robert Jeanne, Chris Starr, Jun-ichi Kojima and two anonymous referees. The research was supported by the Foundation for Research Development and the Communication Biology Research Group of the University of the Witwatersrand.

### References

- Akre, R. D., 1982. Social wasps. In: *Social Insects, Vol. 4* (H. R. Hermann, Ed.), Academic Press, New York: pp. 1–105.
- Freisling, J., 1943. Zur Psychologie der Feldwespe. *Z. Tierpsychol.* 5:438–463.
- Hermann, H. R. and M. S. Blum, 1981. Defensive mechanisms in the social Hymenoptera. In: *Social Insects, Vol. 2* (H. R. Hermann, ed.), Academic Press, New York. pp. 77–197.
- Jeanne, R. L., 1982. Evidence for an alarm substance in *Polistes canadensis*. *Experientia* 38:329–330.
- Jeanne, R. L., in press. The evolution of exocrine gland function in wasps. In: *Natural History and Evolution of Paper Wasps. Proceedings of a Conference held in Florence, Italy, October 1993* (S. Turillazzi and M. J. West-Eberhard, Eds.), Oxford University Press, Oxford.
- Keeping, M. G., 1989. Social biology and colony dynamics of the polistine wasp *Belonogaster petiolata* (Hymenoptera: Vespidae). Ph. D thesis, University of the Witwatersrand, Johannesburg. 414 pp.
- Kojima, J.-I., 1994. Evidence for an alarm pheromone in *Ropalidia romandi* (Le Guillon) (Hymenoptera, Vespidae). *J. Aust. ent. Soc.* 33:45–47.
- Maschwitz, U., 1964. Gefahrenalarmstoffe und Gefahrenalarmierung bei sozialen Hymenopteren. *Z. vergl. Physiol.* 47:596–655.

Received 6 July 1994;  
revised 13 February 1995;  
accepted 23 March 1995.