

## **External stimuli in searching for favourable habitat, overwintering sites and refugia of ground beetles: a short review**

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**Abstract.** More than 10 morphological types and subtypes of sensilla have been found on the antennae of ground beetles. On the basis of their external features and similarity with the antennal sensilla of other insects, it is suggested that they may function as mechano-, olfactory, taste, thermo- and hygroreceptors. In ground beetles, however, a thermoreceptive cell located in antennal campaniform sensilla, and three chemoreceptive cells of four, innervating large antennal taste bristles have been electrophysiologically identified. These cells are the salt, pH and sugar cell. Their probable role in searching for favourable habitats, overwintering sites and refugia is discussed. It is concluded that the strength of external chemosensory stimuli to which antennal taste cells do not fire, or fire at very low frequency, represents chemical conditions in the ground beetles' preferred habitats and microhabitats. In the future, a good knowledge of external stimuli crucial in the searching behaviour of ground beetles' could allow more effective manipulation of these predatory beetles in agricultural lands..

**Key words:** ground beetles, antennal sensilla, morphology, electrophysiology, habitat selection

**Habitat choice.** Ground beetles are abundant in agricultural landscapes all over the world and could be the important natural enemies of a number of agricultural pests. These predatory insects can be effective biological control agents in conditions of sustainable agriculture and integrated pest management (Thiele, 1977; Lövei & Sunderland, 1996; Kromp, 1999; Symondson et al., 2002). Searching for food and favourable environmental conditions lead ground beetles to their preferred habitats, but several different behavioural mechanisms help beetles find or remain in suitable habitats. These mechanisms include daily activity rhythm, sun-compass orientation, and orientation either toward or away from silhouettes. Some riparian ground beetles find their habitat by sensing volatile chemicals emitted by blue algae living in the same habitat. Habitat and microhabitat distribution can be influenced by several factors: temperature and humidity conditions, food availability, presence and distribution of competitors, occurrence of suitable refugia and overwintering sites. Habitat choice is so specific that ground beetles are often used to characterize habitats (Thiele, 1977; Lövei & Sunderland, 1996). In the future, a good knowledge of external stimuli crucial in ground beetles' searching behaviour could allow more effective manipulation of these beetles in agricultural lands. Therefore, the study of the functioning of antennal sensilla in ground beetles was started six years ago in the Department of Plant

Protection of the Estonian University of Life Sciences. A generalization of our results follows.

**Morphology of antennal sensilla.** Several thousands of chaetoid, trichoid, basiconic, campaniform, coeloconic and auricillic sensilla have been found on the ground beetles' antennae. They may sensitively respond to a great variety of mechanical, olfactory and taste stimuli. The antennae of ground beetles are also well equipped with thermo- and hygroreceptors (Kim & Yamasaki, 1996; Merivee et al., 2000, 2001, 2002). The ultrastructure of antennal taste sensilla has been studied in *Nebria brevicollis*. These large bristles have five neurones, one of which terminates in the tubular body and the others are unbranched in the hair; based on that it has been suggested that these sensilla have a dual function: mechanoreception and contact chemoreception (Daly & Ryan, 1979).

**Electrophysiology of antennal thermoreceptors.** For animals as small as insects, microclimatic conditions may be quite disadvantageous, if not lethal, in the absence of instant cues about their temperature and humidity. To avoid temperature extremes, and to find and stay in thermally favourable areas, insects are well equipped with physiologically different kinds of thermoreceptors packaged in many different external cuticular structures. In a number of ground beetles of the tribes Pterostichini and Platynini, single sensillum extracellular recordings demonstrate that tiny antennal campaniform sensilla house a sensitive thermoreceptive cell. By reaction type it is a phasic-tonic cold cell showing remarkable increase of its firing rate in response to temperature decreases of 0.1°C and larger. Maximum peak frequencies at the beginning of the response may reach up to 400–650 Hz depending on the species studied. The first manifestation of rapid warming in the nerve impulse sequence is a very long interspike period, followed by diminished activity. In eurythermic open field ground beetles *Pterostichus cupreus*, *Agonum muelleri* and *Anchomenus dorsalis* the stationary firing rate did not significantly depend on temperature in the range of 23–30°C but plots of firing rate versus temperature showed rapid declines when lethally high temperatures – close to 40°C – were approached. In contrast, a nearly linear decline of the firing rate/temperature curve was observed in stenothermic forest species *Platynus assimilis*, *Pterostichus oblongopunctatus* and *P. aethiops* over the range of 23–38°C. Some conspicuous differences found in the responses of the cold cells can be related to the ecological preferences and daily activity rhythms of the ground beetles studied (Merivee et al., 2003; Must et al., 2006; Must et al., in press).

**Electrophysiology of antennal contact chemoreceptors.** Of four chemoreceptive cells innervating antennal taste bristles in ground beetles, three are identified. These are the salt, pH and sugar cells. All cells show phasic-tonic type of reaction with a pronounced phasic component. In the salt cell, the stimulating effect is dominated by the cations involved, and in most cases, monovalent cations are more effective stimuli than divalent cations (Merivee, et al., 2004). The pH cell did not fire or fired at very low frequency at pH 3–6. As the pH of the stimulus buffer solution increases, higher rates of firing are produced by the pH cell. For example, the number of action potentials elicited by 100 mM phosphate buffer at pH 11 was approximately 16-fold higher compared with that at pH 8, and firing rates during the first second of the

response were 27.9 and 1.7 imp s<sup>-1</sup>, respectively (Merivee et al., 2005). These results suggest that in *P. aethiops*, in its preferred acid forest habitats and overwintering sites in brown-rotted wood at pH 3 to 5, the antennal pH sensitive cell does not discharge or discharges at very low frequency with the first s firing rate close to 1 imp s<sup>-1</sup> or lower. Areas with a higher pH seem to be unfavourable to this insect and when contacted the pH cell signals with a stronger response. This may occur, for example, in places with decaying plant material on the soil surface. Many of the materials composted contain significant amounts of protein, which is converted to ammonia toxic to many organisms and serves as the primary substrate in the nitrification processes. Nitrification processes have been observed at pH levels ranging from 6.6 to 9.7 (Odell et al., 1996). Obviously, the ground beetle *P. aethiops* avoids places with a high pH. These electrophysiological data on functioning antennal salt and pH cells correlate well with behavioural laboratory and ecological field experiments on soil pH and salt content preferences in ground beetles (Thiele, 1977; Paje & Mossakowski, 1984; Irmeler, 2001, 2003).

The third cell of the ground beetles' antennal taste sensilla is a phasic-tonic sugar cell. In *P. aethiops* and *P. oblongopunctatus*, this cell responds to mono- and disaccharides, glucose and sucrose, respectively, over a range of 1–1000 mM whereby the stimulatory effect of sucrose is significantly stronger compared to glucose (Merivee et al., unpublished data; Milius et al., unpublished data). Both sugars are important in plant carbohydrate metabolism (Kruger, 1993). These ground dwelling insects may come into contact with live and decayed plant material anywhere in its habitat, including its preferred overwintering sites in brown-rot decayed wood, which does not contain soluble sugars and cellulose, and which is composed of pure lignin. Therefore, low content of soluble sugars in their overwintering sites and refugia seems to be favourable for these ground beetles.

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