Influence of temperature on host location and multisensory orientation in the parasitoid *Pimpla turionellae* (L.) (Hymenoptera)

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Abstract: Die Schlupfwespe *Pimpla turionellae* parasitiert versteckte Lepidopterenpuppen und orientiert sie sich bei der Wirtssuche multisensorisch mittels visueller Reize und aktiver Vibrationsortung mit selbst produzierten Schwingungen (Vibrational-Sounding). Die Studie untersucht, inwieweit die Wespen bei Änderung der Umgebungstemperaturen von 8-26°C (1) zwischen der temperatur-sensitiven vibratorischen und der -insensitiven visuellen Orientierung wechseln und (2) gegebenenfalls selbst die Körpertemperatur regulieren können, um die sehr präzise Vibrationsortung bei niedrigen Temperaturen aufrechtzuerhalten. Messungen mit Infrarot-Thermographie zeigen, dass suchende Wespen leicht erhöhte Körpertemperaturen während der vibratorischen Wirtssuche aufweisen, welche auf metabolische Wärmeproduktion zurückzuführen sind. Wahlexperimente unter kontrollierten Temperaturen zeigen zudem, dass die Nutzung der temperatur-sensitiven vibratorischen Reize bei pessimalen Temperaturen abnimmt und die Wespen auf fast ausschließliche visuelle Orientierung wechseln. Folglich wird die Relevanz einzelner Reize bei der multisensorischen Orientierung direkt vom Faktor Temperatur beeinflusst. Solange ein zuverlässiger Reiz vorhanden ist, nimmt dabei auch die Präzision der Lokalisation insgesamt nicht ab.

Keywords: Searching behaviour, vibration, vision, thermoregulation, Ichneumonidae, host pupae.

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The ichneumonid wasp *Pimpla turionellae* (L.) (Hymenoptera) is a specialist parasitoid of lepidopteran pupae, and has to overcome the challenge of reduced chemical and visual cues as pupae are immobile, do not feed and do not emit excrements. Certain hymenopteran species have developed a particular mechanosensory mechanism in order to locate hosts hidden in hollow spaces inside of plant material (Broad & Quicke 2000). Similar to echolocation they use self-produced vibrations, instead of sounds, that are transmitted by the antennae onto the substrate. In analogous way to acoustics, this mechanosensory mechanism is referred to as vibrational sounding (Wäckers & al. 1998).

Thermal dependence is well known in acoustical and vibrational communication of arthropods (e.g. Pires & Hoy 1992, Shimizu & Barth 1996) and is likewise presumed to affect mechanosensory host location by vibrational sounding. The species *P. turionellae* has recently been found to use vibrational sounding successfully in a temperature range from 8 to 28°C, but with less performance of searching behaviour and an adjusted signal production at extreme temperatures (Kroder & al. 2006, Kroder & al. 2007b, Samietz & al. 2006).

Many insects have evolved strategies to maintain a balance of body temperature by ecto- and endothermic means. Raising and maintaining body temperatures above the ambient environment by endothermic means is particularly known in several hymenopteran species (Heinrich 1993). In the case of a thermally influenced host location mechanism, such means of thermoregulation could be supposed as well in order to maintain performance with changing temperatures. The study elucidates if the wasps are able to regulate their body temperature at suboptimal conditions during vibrational sounding and furthermore examines the role of vibrational sounding in multisensory orientation at different ambient temperatures.

Material and methods

A laboratory strain of *P. turionellae* was reared on pupae of *Galleria mellonella* (Lepidoptera). Adults were confined in Plexiglas containers and fed with honey and water. The wasps were kept at 15°C, 70% relative humidity (rh) with a photoperiod of 16D:8L.

The body temperature was measured in four temperature treatments at 10°C, 18°C, 26°C and 30°C. Females were observed individually in a Plexiglas box, and a data logger recorded ambient air temperature and relative humidity. A paper cylinder (length: 55 mm, diameter: 8 mm) made of airmail paper containing a cigarette filter (15 x 8 mm) as solid section imitating the hidden host pupa. This experimental approach excluded chemical and visual cues, providing exclusively mechanosensory cues for host location. An infrared (IR) thermography camera transformed the thermal radiation emitted from the insects' surface into electrical impulses, which were amplified producing the so-called thermogrammes consisting of images showing temperature in shades of grey or in colour steps (STABENTHEINER & SCHMARANZER 1987). The surface temperature of the head, thorax and abdomen of each female was measured, as well as the surface temperature at two different points on the paper roll model as ambient surface temperature. Body temperatures of "searching females" (i.e. typical short-range searching behaviour) were compared with "pausing females" (i.e. no visible activity).

The effect of ambient temperature on multisensory orientation was tested at 18°C and at the extreme temperatures of 8 and 28°C where *P. turionellae* still employs vibrational sounding but with a significantly lower precision (SAMIETZ & al. 2006). The paper-cylinder (length: 125 mm, diameter: 8 mm) contained the cigarette filter as solid section and a black band as visual cue imitating damages by a potential host. The black band was printed on the airmail paper with a copier (output: 1200 dpi). In this experimental approach host location of the wasps is restricted to vibrational and visual cues. Thus, ovipositor insertions can be attributed to vibrational and visual orientation. Each female was individually exposed to a plant-stem model for 20 minutes in a Plexiglas box. For the analysis, plant-stem models were subdivided into 34 sections with section widths of 3.7 mm. This allowed scoring the position of the insertions relative to the two different cues on the plant-stem model (KRODER & al. 2007a).

All statistical analyses were conducted by using the statistical computation language R.

Results

The body temperatures of head and thorax in the pausing wasps were significantly higher than the ambient surface temperature at 10°C and significantly lower at 26°C and 30°C (Fig. 1).

Searching females showed body temperatures above ambient temperature in all temperature treatments (Fig. 1). Head, thoracic and abdomen temperatures of searching females differed from ambient surface temperature by 0.21 ± 0.07°C (mean ± SEM), 0.30 ± 0.09°C and 0.17 ± 0.06°C respectively averaged over all four treatments.

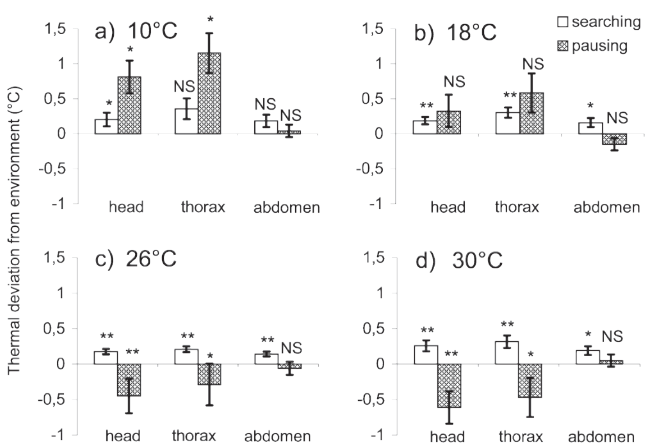

Fig. 1: Thermal deviation from environment (i.e. ambient surface temperature) of head, thorax and abdomen of searching (blank) and pausing females (chequered) at 10°C (a), 18°C (b) 26°C (c) and 30°C (d).
Bars and error bars show the mean values and the standard deviations. Significant differences from ambient surface temperature tested by One sample *t*-test (NS, not significant; *, $P < 0.05$; **, $P < 0.01$).

During multisensory orientation, the two cues on the plant-stem model showed a strong influence on host location behaviour of the female wasps (Fig. 2). The overall precision of the parasitoids host location was not affected by ambient temperature (Fig. 2; Kruskall-Wallis H-test). They inserted their ovipositor with an average deviation (mean ± SD) from the cue centres of 1.26 ± 0.96 section widths in total.

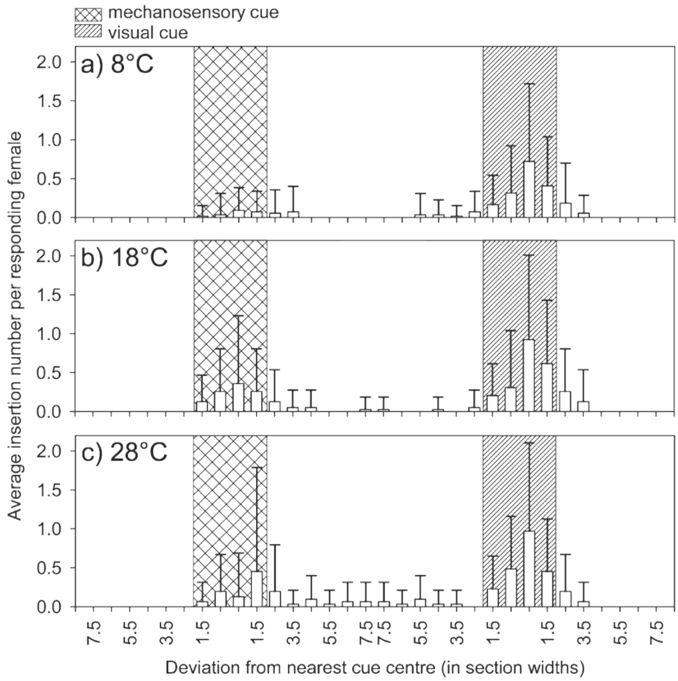

Fig. 2: Distribution of ovipositor insertions of *Pimpla turionellae* on plant-stem model with mechanosensory (cigarette filter) and visual cue (black band) at 8 (a), 18 (b) and 28°C (c). The bars and error bars show average number of insertions per responding female in each section (mean ± SD).

Focussing on the females with at least three insertions, a significant temperature effect was noted on the relative importance of the vibrational cue but not on the visual cue (Kruskal-Wallis *H*-test). At the low temperature of 8°C, the relative importance of vibrational sounding nearly disappeared. By contrast, the highest relative importance of the visual cue was found at 8°C, and the use of the two cues differed significantly at 8 and 28°C (Fig. 3). At the medium temperature of 18°C both cues, vibrational and visual orientation, were equally used during host location by female wasps.

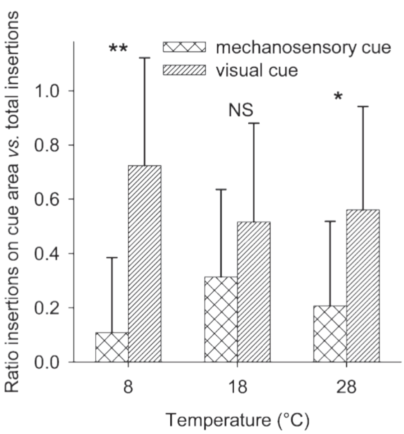

Fig. 3: Ratio between number of ovipositor insertions on cue areas and total number of insertions revealing the relative importance of mechanosensory (mean ± SD) and visual cue in *Pimpla turionellae* at 8, 18 and 28°C. Only females responding with at least three ovipositor insertions were included into this analysis. Asterisks indicate significant differences between vibrational and visual cue by Wilcoxon Signed Ranks test (NS, not significant; *, $P < 0.05$; **, $P < 0.01$).

Discussion

The measurements on the body temperature of *P. turionellae* during host location by vibrational sounding itself showed no evidence for a temperature-regulated body. The infrared recordings of pausing females, by contrast, revealed body temperatures that are slightly warmed up at cold ambient temperatures and cooled down at hot ambient conditions. Vibrational sounding probably conflicts with these endothermic mechanisms as regulation only occurs in non-searching females. In nature, *P. turionellae* may furthermore regulate its body temperature by behavioural means, which could be combined with the observed low-level endothermy in pausing phases. In behavioural observations, the host-location process was more often discontinued under suboptimal conditions, which could be also caused by thermoregulatory requirements of the wasps (S. Kroder, J. Samietz, A. Stabentheiner, S. Dorn, unpubl.).

In extreme cold and extreme warm environments within their activity range, the wasps fail to detect potential hosts with a sufficient precision (SAMIETZ & al. 2006). The reliability of vibrational cues declines at these temperatures, and the role of vibrational sounding in a multisensory orientation accordingly decreases. Under suboptimal conditions, wasps switch from the use of multiple cues to the single use of the more reliable visual cue. The varying relative importance has so far been focused on the dependence on the range of host location (VÖLKL 2000). Based on our results, relative importance of cues does not only vary in spatial scales. The simultaneous use of several information sources not only improves the reliability, it also enables parasitoids to keep accuracy and efficiency of host location despite of changing abiotic factors (KRODER & AL. 2007A). Hence, due to multisensory orientation, searching behaviour is not restricted to possibly narrow windows of environmental conditions for the use of single information sources.

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