SHORT COMMUNICATION

Effect of ambient temperature on mechanosensory host location in two parasitic wasps of different climatic origin

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Abstract. Several parasitic wasps of the Pimplinae (Ichneumonidae) use selfproduced vibrations transmitted through plant substrate to locate their concealed immobile hosts (lepidopteran pupae) by reflected signals. This mechanosensory mechanism of host location, called vibrational sounding, depends on the physical characteristics of the plant substrate and the wasp's body and is postulated to depend on ambient temperature. Adaptations of two parasitoid species to thermal conditions of their habitats and the influence of temperature on the trophic interaction during host location are investigated in the tropical Xanthopimpla stemmator (Thunberg) and compared with the temperate Pimpla turionellae (L.). Plant-stem models with hidden host mimics are offered to individual wasps under defined temperature treatments and scored for the number and location of ovipositor insertions. Significant effects of temperature are found on host-location activity and its success. The tropical species possesses an optimum temperature range for vibrational sounding between 26 and 32 °C, whereas the performance decreases both at low and high temperatures. The temperate species reveals substantial differences with respect to performance at the same thermal conditions. With increasing temperature, P. turionellae shows a reduced response to the host mimic, reduced numbers of ovipositor insertions, and decreased precision of mechanosensory host location. In the tropical X. stemmator, the female wasps are able to locate their host with high precision over a broad range of ambient temperatures, which suggests endothermic thermoregulation during vibrational sounding. Environmental physiology may therefore play a key role in adaptation of the host location mechanism to climatic conditions of the species' origin.

Key words. Echolocation, host location, parasitoid, temperature, vibration, vibrational sounding.

Introduction

Temperature is one of the most important environmental parameters for all organisms. It affects nearly all biological processes, rates and functions and its influence on metabolism and cellular biochemical processes is well understood (Willmer *et al.*, 2000). Temperature tolerance can vary considerably and has significant behavioural and ecologicalimplications especially in poikilothermic animals such as insects (Hausmann *et al.*, 2005; Samietz *et al.*, 2005). Nevertheless, knowledge is limited about the influence of temperature on species interactions and, accordingly, on adaptations of prey- or host finding mechanisms in insects. Most of the respective current work is focused on the influence of environmental temperature on the interaction

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between plants and herbivores (Bale *et al.*, 2002; Richardson *et al.*, 2002; Kührt *et al.*, 2005). Particularly rare are studies considering the influences of varying temperature conditions on multitrophic systems or between herbivores and the highly important parasitoid guild. Some studies reveal significant effects of temperature on parasitation rates (Benrey & Denno, 1997) or on the amount and quality of volatiles that are potentially effective on parasitoids' behaviour (Gouinguené & Turlings, 2002; Vallat *et al.*, 2005). However, the consequences for host location by parasitic wasps and how the senses used during host location are affected remain mostly unknown.

Successful parasitism requires an effective host location mechanism by the parasitoid. Depending on the senses involved, certain mechanisms of host location are more likely to be influenced by temperature than others. Influence of temperature is especially relevant in mechanosensory mechanisms of host location, such as the vibrational sounding found in several species of hymenopteran parasitoids, because such mechanisms depend on physical properties of the environment and on the physical activity of the insects (Fischer et al., 2001; Otten et al., 2002; Fischer et al., 2003, 2004). During vibrational sounding, female wasps transmit self-produced vibrations on solid plant material and locate their immobile pupal hosts hidden within the plant substrate by the sensed signal modifications (Wäckers et al., 1998; Broad & Quicke, 2000). A direct myogenic origin of the wasps' vibrations has been suggested from observations in previous studies (Henaut, 1990; Otten et al., 2002; H. Otten, F. Wäckers & S. Dorn, unpublished data). Due to the power output of insect muscles being affected by temperature (Hosler et al., 2000; Josephson et al., 2000; Sueur & Sanborn, 2003), thermal dependence of vibrational signals during mechanosensory host location can be expected. Additionally, the vibrational signals are sensed with subgenual organs as mechanoreceptors in the parasitoid's tibiae (Otten et al., 2002) and, because the efficiency of mechanoreceptors is also influenced by temperature (Coro et al., 1994; Hoger & French, 1999; Franz & Ronacher, 2002), a temperature effect on the receiving side of the sensory system can be postulated.

In the present study, two species of pupal parasitoids (Hymenoptera: Ichneumonidae) with different climatic origins are chosen to test the thermal dependence of vibrational sounding. Xanthopimpla stemmator (Thunberg) originated from the palaeotropical regions of Asia and successfully colonized African as well as tropical American regions (Moore & Kfir, 1996). The species uses vibrational sounding in multisensory orientation and parasitizes lepidopteran stemborers (Fischer et al., 2004). Pimpla turionellae (L.) is widely distributed in temperate woodlands of the Palaearctic (Bogenschütz, 1978) and is well studied with respect to mechanosensory host location (Fischer et al., 2001; Otten et al., 2001; Fischer et al., 2003). According to the distribution, it is expected that the two species have distinct temperature ranges of effective vibrational sounding. In the present study, the temperature range in which X. stemmator uses vibrational sounding successfully is studied and a comparison made of two differently adapted species, reflecting the thermal conditions of the habitats to which they are adapted. The success of vibrational sounding is examined by offering plant-stem models with hidden host mimics to individual wasps, excluding visual and chemical cues in laboratory treatments under controlled ambient temperatures.

Materials and methods

Parasitoid rearing

Laboratory strains of X. stemmator and P. turionellae were reared on pupae of Galleria mellonella (Lepidoptera). Adults were confined after emergence in Plexiglas containers $(25 \times 25 \times 25 \text{ cm})$ fed with honey and water and were allowed to mate. The wasps were kept at 23 °C and 70% relative humidity (RH) in photophase and at 15 °C and 80% RH in scotophase under an of LD 16:8 h photoperiod. The host pupae were exposed three times a week for ovipositing and host feeding. Parasitized pupae were stored at 24 °C and 60% RH under an LD 16 : 8 h photoperiod until the emergence of adults. The strain of X. stemmator originated from the University of Illinois at Urbana-Champaign, Illinois, in 2000 and has been maintained as described above from that date onwards. The strain of P. turionellae was obtained in 1994 from the Forest Research Institute of Baden-Württemberg, Germany, and has been kept at 15 °C and 70% RH under an LD 16 : 8 h photoperiod before the generation used in the present experiments.

Plant-stem model

The females of the two parasitoid species attempt to insert their ovipositor into various hollow rounded substrates. A paper cylinder (length 125 mm, diameter 8 mm) made of airmail paper (ELCO Atlantic Clipper Air Mail, 45 g/m², Allschwil, Switzerland) containing a cigarette filter $(15 \times 8 \text{ mm}, \text{Gizeh}, \text{Gummersbach}, \text{Germany})$ as solid section imitated the hidden host pupa. This experimental approach allowed solely mechanosensory cues to be offered, excluding chemical and visual cues. Hence, directed orientation can be attributed to vibrational sounding. Such plant-stem models have been used successfully in a number of studies on host location in these insects (Otten *et al.*, 2001; Fischer *et al.*, 2003).

Experimental design

The females were tested after maturation, which is reached typically after 25 days in *X. stemmator* females, and after 7 days in *P. turionellae* females. The wasps were allowed to mate before the experiments and had host

contact for the first time 24–48 h before the experiments started.

The experiments were performed individually in Plexiglas containers $(18.5 \times 8.5 \times 7.5 \text{ cm})$ with one plant stemmodel glued on a white background. Due to the distinct host niches, the stem-models had to be positioned vertically in the trials with *X*. stemmator and horizontally in the trials with *P*. turionellae.

At least 1 h before the experiments, the animals were acclimated to the test conditions (i.e. the respective temperature and 60% RH). Each trial lasted 20 min and at most five females were tested simultaneously in separate containers. All female parasitoids and stem-models were used only once. Accordingly, each model is associated with one female for the subsequent analysis.

Host location by vibrational sounding in X. stemmator females was investigated at seven temperature treatments from 22 to 34 °C in 2 °C increments. Outside this range (i.e. at 20 and 36 °C), no wasp of the tropical species showed a positive response with oviposition activity. Exposure to temperatures of 38 °C and higher during acclimation and the experiment (totalling up to 1.5 h) led to a 100% mortality (n = 5 females, S. Kroder, personal observation). The desired sample size of responding females was 20 for each of the seven temperature treatments.

Furthermore, as a basis for direct comparison of the tropical and the temperate species in the overlapping part of the temperature ranges, females of *P. turionellae* were tested for their performance with respect to mechanosensory host location at 22, 26 and 30 °C. Both species were reared under the same temperature conditions. The desired sample size of responding females was 30 for each species in each of the three temperatures to allow direct comparison.

A total number of 807 *X. stemmator* females were tested over the seven temperature treatments from 22 to 34 °C. A total of 241 individuals of *P. turionellae* were tested for direct comparison with the tropical species for the temperature treatments at 22, 26 and 30 °C.

Data analysis

The success of mechanosensory host location by the parasitoids was quantified by scoring the number, location, and precision of ovipositor insertions on the plant-stem model in relation to the hidden host mimic. The stemmodels were subdivided into 34 sections (section width 3.7 mm). The cigarette filter as host mimic was located in section 20–23. This allowed scoring of the position of insertions relative to the host mimic. For each treatment and species, the responsiveness as the proportion of ovipositing females, the quantitative insertion activity as the average number of ovipositor penetrations per responding female, and the precision of ovipositor insertions with respect to the host mimic using vibrational sounding as the location mechanism were analysed.

Two parameters were used to compare the precision of mechanosensory host location between the different

temperature treatments with X. stemmator, as well as between the two species tested. First, the bias of host location was quantified as the absolute mean deviation of individual insertions from the centre of the host mimic. Second, the scattering of host location was quantified by the variance of the insertion positions of each individual female.

Significant differences in the general responsiveness of the females among the different treatments were analysed separately in both species using χ^2 tests. The influence of temperature on quantitative insertion activity in *X. stemmator* and in *P. turionellae* was analysed by Kruskal–Wallis tests due to the nonparametric distributions of these data.

For the comparison between *X. stemmator* and *P. turionellae*, the quantitative insertion activity was evaluated for each temperature treatment by Mann–Whitney *U*-tests.

The temperature influence on the two precision parameters in X. *stemmator* was analysed by analyses of covariance (ANCOVA) with the covariate body weight (standardized). To achieve a normally distributed data set, the variance of the insertion positions was log-transformed (natural logarithm).

Both precision parameters were compared between the tropical and the temperate species by two-way ANCOVA with the factor species, the factor temperature treatment and covariate body weight (standardized). All analyses were performed with the software SPSS 12.0.1 for Windows (SPSS Inc., Chicago, Illinois).

Results and discussion

The temperature range allowing for an effective vibrational sounding in the tropical species X. stemmator lies between 22 and 34 °C, whereas the use of this mechanosensory host location is not successful at temperatures below 22 and above 34 °C (Fig. 1). Over all treatments, X. stemmator shows an average proportion of females responding to the host mimic with ovipositor insertions (responsiveness) of $23.9 \pm 9.4\%$ (mean \pm SD). The general responsiveness of the females differs significantly between the temperature treatments ($\chi^2 = 30.9$, d.f. = 6, P < 0.001) with the highest value of 35.7% at 32 °C. The responsiveness declines by more than 20% with temperature increasing from 32 (35.7%) to 34 °C (13.7%). By contrast, the temperature range allowing for an effective vibrational sounding in the temperate species P. turionellae is broader, extending from 8 to 32 °C, with a peak at 18 °C, as found in an associated study (Samietz et al., 2006). To directly compare insertion activity and precision parameters between the two species, a temperature range of 22-30 °C was chosen in which both species engage readily in vibrational sounding on the plantstem model with a hidden host mimic. Even within this relatively narrow range, ambient temperature influences the responsiveness of the temperate parasitoid P. turionellae $(\chi^2 = 25.7, d.f. = 2, P < 0.001)$, with the lowest temperature tested yielding the largest proportion of responding



Fig. 1. Responsiveness of *Xanthopimpla stemmator* at seven temperature treatments from 22 to 34 °C (grey) and of *Pimpla turio-nellae* at three temperature treatments at 22 °C, 26 °C and 30 °C (white). Responsiveness is quantified as the percentage of females responding to the plant-stem model with at least one ovipositor insertion.

females (60.8%) and the highest temperature tested yielding the lowest proportion (26.0%), giving an average responsiveness of 44.5 \pm 19.0% (mean \pm SD) over all temperatures tested (Fig. 1). Although the temperate species has been reported to parasitize concealed lepidopteran pupae in orchards already in May and June in Switzerland (Mani *et al.*, 1986), where temperature can easily drop to 8 °C and occasionally exceed 30 °C, the tropical species fails to engage substantially in vibrational sounding at temperatures below 22 °C, which are not typical for its habitat (Moore & Kfir, 1996).

Furthermore, temperature significantly influences the insertion activity in the tropical (Kruskal-Wallis test; $H_6 = 22.0, P = 0.001$) as well as in the temperate species (Kruskal–Wallis test; $H_2 = 7.57$, P = 0.023) (Fig. 2). The ovipositor insertion activity varies from one to a maximum of 41 individual insertions per female in X. stemmator and from one to 32 individual insertions per female in P. turionellae. The lowest activity in X. stemmator females (mean \pm SE) is at 22 °C with 5.17 \pm 0.71 insertions and the highest activity is at 32 °C with 13.05 \pm 1.57 insertions (Table 1). By contrast, P. turionellae shows the lowest insertion activity at 22 °C with 5.00 \pm 0.72 insertions and the highest activity at 26 °C with 8.71 \pm 1.04 insertions. When comparing the tropical with the temperate species, the mean number of insertions per female differs at 30 °C (Mann–Whitney U-test; Z = -2.42, P = 0.016), but not at 22 and 26 °C (Mann–Whitney U-test; 22 °C: Z = -0.102, P = 0.92; 26 °C: Z = -0.289, P = 0.77). Although responsiveness to the host mimic and quantitative insertion activity of P. turionellae declines with increasing temperature from 22 to 30 °C, activity increases in X. stemmator peaking at 32 °C, even though both species were reared under



Fig. 2. Quantitative insertion activity as the mean number of insertions per responding female of *Xanthopimpla stemmator* (grey) and *Pimpla turionellae* (white) at three temperature treatments. The box shows the 25th and 75th percentile with median (solid line) and mean (dashed line); error bars show the 10th and 90th percentiles.

the same conditions during the experiments. The origin of X. stemmator is characterized by ambient temperatures around 30 °C with no large seasonal variances (Moore & Kfir, 1996). The range of the response in the present study pivots around this value in this tropical species and data with respect to ovipositor insertion activity show a clear maximum at these temperatures.

Distinct temperature thresholds for vibrational sounding are evident in the precision of the ovipositor insertions. The bias of mechanosensory host location (Fig. 3) differs significantly between the tropical and the temperate species (ANCOVA factor species: $F_{1,182} = 8.67$, P = 0.004). Xanthopimpla stammator females inserted the ovipositor closer to the cue centre than P. turionellae females at all three temperatures compared in the present study. Nevertheless, neither the temperature nor body weight has a significant effect on the bias (ANCOVA; factor temperature: $F_{2,182} = 2.81$, P = 0.063; covariate body weight: $F_{1.182} = 0.270$, P = 0.60). The scattering is not affected by temperature and does not differ significantly between species (ANCOVA; factor species: $F_{1,150} = 0.412$, P = 0.52; factor temperature: $F_{2,150} = 1.41$, P = 0.25). Furthermore, the factors species and temperature show no significant interactions in the two parameters of precision (ANCOVA interaction; bias: $F_{2,182} = 1.63$, P = 0.20; scattering: $F_{2.150} = 0.409, P = 0.67$).

A remarkable aspect of the results obtained in the present study is that the precision of mechanosensory host location can be maintained over a relatively broad range

Treatment (°C)	п	Quantitative insertion activity			
		Mean	Median	Bias	Scattering
Xanthopimpla stemma	tor				
22	30	5.17 ± 0.71	5.0	1.65 ± 0.37	7.95 ± 1.96
24	20	6.15 ± 1.38	4.5	2.55 ± 0.72	10.52 ± 3.81
26	30	8.80 ± 1.30	6.5	1.26 ± 0.20	11.98 ± 2.21
28	20	11.95 ± 2.22	9.5	1.66 ± 0.30	9.50 ± 2.79
30	30	10.77 ± 1.52	9.0	1.69 ± 0.27	13.10 ± 2.61
32	20	13.05 ± 1.57	12.5	2.52 ± 0.55	20.80 ± 4.21
34	20	9.55 ± 2.26	6.5	1.94 ± 0.45	15.71 ± 3.40
Pimpla turionellae					
22	31	5.00 ± 0.72	4.0	1.85 ± 0.34	12.11 ± 2.84
26	31	8.71 ± 1.04	8.0	2.18 ± 0.34	20.35 ± 3.45
30	30	6.87 ± 1.44	4.0	3.50 ± 0.73	18.45 ± 4.99

Table 1. Quantitative insertion activity as the mean number of insertions (\pm SE) per responding female and median, bias of host location quantified as the absolute mean deviation (\pm SE) of individual insertions from the centre of the host mimic (expected value at 21.5 section widths) and mean scattering of host location (\pm SE) as the variance of insertions' position (in section widths) of *Xanthopimpla stemmator* at seven temperature treatments and of *Pimpla turionellae* at three temperature treatments.

of temperatures. Over all treatments in which females of X. stemmator respond positively to the host mimic, there is no significant effect on the bias of mechanosensory host location (i.e. absolute mean deviation of insertions), as well



Fig. 3. Bias of host location quantified as the the absolute mean deviation of individual insertions from the centre of the host mimic (expected value at 21.5 section widths) of *Xanthopimpla stemmator* (grey) and of *Pimpla turionellae* (white) at three temperature treatments. The box shows the 25th and 75th percentile with median (solid line) and mean (dashed line); error bars show the 10th and 90th percentiles.

as no interaction between the factor and the covariate (ANCOVA; factor temperature: $F_{6,170} = 1.10$, P = 0.37; covariate body weight: $F_{1,170} = 3.47$, P = 0.064; interaction: $F_{6,170} = 0.705$, P = 0.65). In addition, temperature does not affect the scattering of mechanosensory host location (i.e. variance of ovipositor insertion positions) (ANCOVA; factor temperature: $F_{6,141} = 0.815$, P = 0.56; covariate body weight: $F_{1,141} = 0.645$, P = 0.58). Again, no interaction between temperature and body weight is found (ANCOVA interaction: $F_{6,141} = 1.94$, P = 0.080). In X. stemmator, the highest values (mean \pm SE) of bias (2.52 \pm 0.55 section widths) and scattering (20.8 \pm 4.2 section widths) are recorded at 32 °C (Table 1). The lowest values of bias $(1.65 \pm 0.37 \text{ section widths})$ and scattering (7.95 ± 1.96) section widths) are found at 22 °C. The temperate species again shows a broader range of equal precision of vibrational sounding from 10 to 24 °C, but a steep and significant decline below and above those temperatures (Samietz et al., 2006). By analogy to the evolution of vibrational sounding in two hymenopteran families under a variety of ecological conditions (Broad & Quicke, 2000), it is concluded that this mechanism of mechanosensory host location is adapted strictly to the temperature range encountered in multitrophic species interactions by the parasitoid species under consideration.

The precision of the sensory mechanisms investigated in the present study depends on the female wasps' ability to produce and receive signals for use in vibrational sounding. Temperature dependence is known with respect to vibration production in spiders (Shimizu & Barth, 1996) and with respect to the physically familiar sound production of crickets (Martin *et al.*, 2000) and cicadas (Fonseca & Revez, 2002). The efficiency of mechanoreceptors as a second part of the sounding system is also influenced by ambient temperature. Many studies report a thermal effect on mechanotransduction, action potential encoding, and action potential conduction in arthropods (French, 1985; Hoger & French, 1999; Franz & Ronacher, 2002). However, the pupal parasitoids appear to cope efficiently with the constraints caused by changes in temperature. Both species, P. turionellae and X. stemmator, use vibrational sounding for host location successfully over a broad range of environmental temperatures. The discrepancy between the expected temperature effect on vibration and the observed performance of the wasps might be due to a separate mechanism for the regulation of body temperature permitting a correct functioning of vibrational sounding. In bees, flight muscle temperature is increased by endothermic shivering performed at low ambient temperatures (Heinrich & Kammer, 1973; Stabentheiner et al., 2003). A wing fluttering during host location behaviour is also noted in females of the two wasp species (S. Kroder, personal observation), suggesting that the wasps use endothermic heat production to maintain a balance of body temperature. Another explanation for the broad thermal range of the sensory mechanism could be a temperature coupling system, as is known for cricket- and grasshopper acoustic communication. As the chirp rate and syllable rate of the males' song increase with higher temperature, the females' phonotactic preference on the receiving side changes accordingly (Bauer & von Helversen, 1987; Pires & Hoy, 1992).

In conclusion, the performance of mechanosensory host location by vibrational sounding in the two ichneumonid pupal parasitoids investigated in the present study is markedly influenced by ambient temperature. Optimum temperature ranges for key behavioural parameters differ between the tropical wasp X. stemmator and the temperate wasp P. turionellae, reflecting the climatic conditions of their natural habitats. Mechanosensory host location is more effective within, or even limited to, the temperature ranges that correspond to the origin of each species. The tropical wasps are able to maintain the performance of their mechanosensory host location over a broad range of temperatures in which insertion precision is not affected. Further studies are required to investigate how the success of mechanosensory host location is maintained in detail over the broad temperature ranges found in the present study. This could be addressed by investigating the vibratory signals in the time and frequency domain under different environmental conditions, and by studying possible mechanisms of behavioural or physiological thermoregulation.

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