

## Article

# Heat stress during development makes antlion larvae more responsive to vibrational cues

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## Abstract

We investigated the effects of heat stress on the responsiveness to vibrational cues, our measure of perceptual ability, in *Myrmeleon bore* antlion larvae (Neuroptera: Myrmeleontidae). We reared these trap-building predatory larvae under 2 heat stress regimes (mild, 30°C, and harsh, 36°C), and after they progressed from one instar stage to another, we tested their perceptual ability in common unchallenging conditions. We hypothesized that exposure to the harsh heat stress regime would impose costs resulting in handicapped vibration responsiveness. We found that the harsh heat stress regime generated more stressful conditions for the larvae, as evidenced by increased mortality and postponed molting, and the loss of body mass among larger larvae. Furthermore, among the individuals who remained alive, those originating from the harsh heat stress regime were characterized by higher vibration responsiveness. Our results suggest 2 not mutually exclusive scenarios. Costly heat stress conditions can sieve out individuals characterized by poor perceptual ability or surviving individuals can attempt to hunt more efficiently to compensate for the physiological imbalance caused by heat stress. Both of these mechanisms fit into the ongoing debate over how adaptation and plasticity contribute to shaping insect communities exposed to heat stress.

**Key words:** antlion, *Myrmeleon bore*, heat stress, perception, trap-building, vibration.

Habitats impose selective pressures that drive multigenerational genetic changes leading to the origin of adaptations or affect organisms more immediately by inducing phenotypic responses of genotypes that help to maximize Darwinian fitness (Pigliucci 2001). For ectotherms such as insects, the primary element of selective conditions that “affects everything that an organism does” is certainly the thermal environment, with its strong effects on body temperatures and thus physiological rates (Clarke 2003). Indeed, environmental temperatures affect ectotherms on every imaginable scale, including an array of different fitness costs, with the first and foremost cost being energy expenditure (Angilletta 2009). While the thermal dependence of ectotherms’ physiology and performance has been extensively studied, we know surprisingly little about how thermal conditions

influence the way that ectotherms sense environmental states and respond behaviorally to environmental cues.

Addressing this important perspective, we performed a laboratory experiment on the sit-and-wait predatory antlion larvae *Myrmeleon bore*, investigating the effects of heat stress (mild vs. harsh) during development on larval responses to sand vibrations that mimicked cues released by the approaching potential prey (small invertebrates such as ants; Guillet et al. 2009). We considered that heat stress imposes physiological costs, which would limit resource availability for the processes involved in the development and maintenance of perceptual abilities. Therefore, we hypothesized that the larvae with a prior experience of our harsh heat stress conditions would become perceptually handicapped, responding less

vigorously to sand vibrations compared with the antlions from mild heat stress conditions (our “trade-off hypothesis”). Alternatively, physiological costs associated with heat stress can increase energetic imbalance, resulting in increased feeding motivation. Given this alternative scenario, we hypothesized that the larvae originating from our harsh heat stress conditions would be characterized by increased stimulation by sand vibrations compared with the other group (our “motivation hypothesis”).

Antlions (Neuroptera: Myrmeleontidae) spend a larger part of their life cycle as larvae, and in many species, such as *M. bore* studied here, larvae remain largely sedentary as sit-and-wait predators (Scharf and Ovadia 2006; Scharf et al. 2011) that build cone-shaped traps in the sand for hunting small invertebrates such as ants (Jingu and Hayashi 2018; Turza et al. 2020). Sedentary lifestyle, hunting mode, and habitat preferences make antlion larvae an excellent research object to study the link between thermal stress and behavioral responses to environmental cues. Most antlion species, including our study species, inhabit arid and open sandy areas, where they are temporarily exposed to extreme heat combined with low humidity and unreliable food availability (Rotkopf et al. 2012; Antoń et al. 2018; Farji-Brener and Amador-Vargas 2020). There is evidence to show that these challenging conditions significantly affect different aspects of antlion biology, such as the levels of behavioral plasticity and life history traits (Klokočovnik et al. 2016; Miler et al. 2020). As larvae, antlions offer a unique opportunity to study the effect of stressful conditions acting on behavior early in development, which can be valuable considering that juvenile organisms are often regarded as more susceptible to environmental stress than adults (Burggren 2018). Finally, although trap-building insects are generally characterized by a limited capacity to actively investigate their surroundings (Katz and Scharf 2018; Scharf et al. 2020), antlion larvae can perceive sand vibrations (Mencinger 1998; Devetak 2005; Devetak et al. 2007; Fertin and Casas 2007; Mencinger-Vračko and Devetak 2008; reviewed in Devetak 2014), which seems to be an important element of their hunting strategy. Larvae show anticipatory movement aiding their hunting (e.g., they adjust position inside the trap, toss sand particles by rapidly flicking their heads) after detecting vibrations indicative of approaching prey and submerge in the sand after detecting startling vibrations.

## Materials and Methods

In June 2020, we collected second-instar larvae of *M. bore* antlions (Poland, coordinates: 50°20'24"N, 19°32'20"E), identified following Badano and Pantaleoni (2014) key for European Myrmeleontidae. We then housed them individually in the laboratory in cups (5 cm in diameter, 4 cm in height) half filled with sand. We performed a laboratory experiment that comprised 2 steps. In the first step, we evaluated heat tolerance in larvae (48 in total) to define 2 heat stress regimes, mild and harsh, for the main part of the study. In the next step (the main part), we exposed larvae (100 in total) to either mild or harsh heat stress for a prolonged time during development, collecting information on their mortality and body mass changes. Then, after releasing the larvae from the stressful conditions, we examined how the experience of the 2 heat stress levels affected their responsiveness to vibrational cues (our measure of perceptual ability).

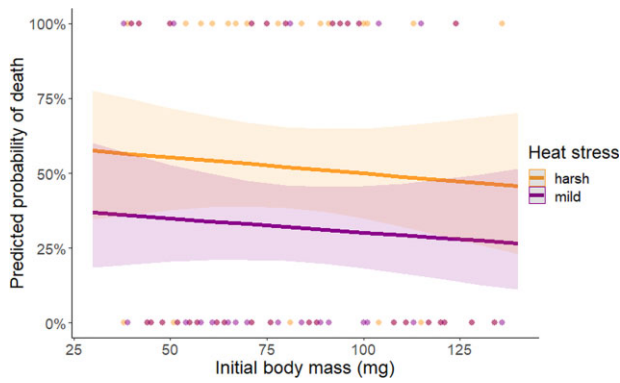
### Finding mild versus harsh heat stress

We performed 2 thermal performance tests on a subset of larvae ( $N=24$  in each test) following established methods and our

previous research on another antlion species (Miler and Czarnoleski 2021). The first test recorded the temperatures chosen freely by larvae exposed to a thermal gradient. The second test recorded the temperatures at which larvae displayed the loss of righting reflex (LORR) when exposed to a steadily increasing temperature. Both tests were conducted on the same day in a climatically controlled room (25°C, full artificial illumination). In the first test, we exposed the larvae individually to a thermal gradient inside an aluminum rail (length: 120 cm) placed on a cooling/heating platform (length: 150 cm) (Biospekt, Kraków, Poland) with an operational gradient inside the rail ranging from 22°C to 44°C and changing linearly by approximately 2.0°C per 10 cm. We covered the bottom of the rail with a thin layer of dry sand (~0.5 cm), placed a single larva on the substrate in the rail at the hot end of the gradient, and covered the rail with transparent foil for isolation. After 15 min, we evaluated the position of the larva along the gradient and recorded the temperature in the sand next to the animal to the nearest 0.1°C using a fast-response thermocouple thermometer (Delta OHM, Selvazzano Dentro, Italy). In the second test, we exposed larvae to a steadily increasing temperature in a water bath (Memmert, Büchenbach, Germany). We placed the larvae singly into individual containers with the bottom covered with a thin layer of dry sand (~0.5 cm) and then placed the containers in a water bath (25°C). Then, we turned on the heat, which resulted in the temperature rising linearly by approximately 1.2°C per min until it reached 46°C. Using a thermocouple thermometer once again, we recorded the temperature in the sand occupied by the larva at the point when the larva showed the LORR, which was preceded by a sudden burst in larval mobility. The 2 tests enabled us to calculate 2 mean temperatures, the first defining the preferred temperatures in the gradient and the second defining the LORR in the water bath (mean  $\pm$  SD: 40.5  $\pm$  1.5°C and 46.0  $\pm$  1.2°C, respectively). We used these statistics as the basis for establishing mild and harsh thermal regimes for the second step. However, because our earlier research demonstrated that even periodical daily exposure to 40°C might be somewhat stressful, especially to second-instar antlion larvae (Miler et al. 2020) and considering that, in the main part of our study, we aimed to expose larvae to thermally stressful conditions for a prolonged time (see the next section), we decided to use 30°C and 36°C for our mild and harsh heat stress regimes, respectively.

### Effects of heat stress on perception

Before entering heat stress regimes, each larva was weighed to the nearest 0.001 g on an electronic balance (Mettler Toledo, Warszawa, Poland), which served as a measure of the initial body mass. To prevent random bias in the average body masses of the larvae exposed to the 2 experimental regimes (mild vs. harsh), we sorted the larvae according to their initial body mass (mean  $\pm$  SD: 82.2  $\pm$  29.3 mg), creating 50 sets of larvae with similar body masses (2 larvae per set). We allocated 1 larva from each set to 1 of the 2 heat stress regimes, which were established in thermal cabinets (Pol-Eco Aparatura, Wodzisław Śląski, Poland) set to 2 constant temperatures (30°C or 36°C for mild or harsh regimes, respectively) and darkness. We housed all larvae in labeled cups (5 cm in diameter, 4 cm in height) half filled with sand. Starting from the first day of the exposure of larvae to heat stress regimes, we fed the larvae once daily with a single *Lasius niger* ant worker according to their activity status (active/inactive) (Miler et al. 2020). We considered active larvae to be those that 1) maintained pitfall traps (i.e., functional and undisturbed) and 2) were visible (i.e., mandibles protruding from the bottom of the trap). We

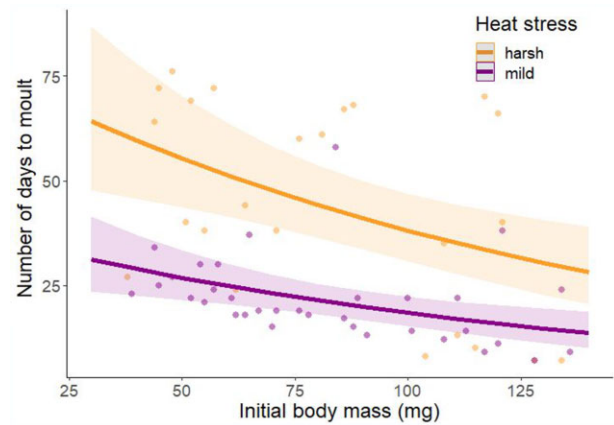


**Figure 1.** Probability of death under the heat stress regimes (mild, 30°C, or harsh, 36°C) in relation to the initial body mass. Lines represent model predictions, with shading indicating estimated 95% confidence intervals.

checked each inactive larva for signs of life functions by digging out and gently prodding the larva with forceps. We left live inactive larvae in their cups, whereas dead inactive larvae were discarded. Each day, we took larvae that reached their third instar stage (i.e., molted) out of the cabinets in which they experienced heat stress regimes, weighed them to obtain their final body mass, and placed them individually into an aluminum box half filled with sand. The boxes with larvae were put in laboratory conditions (constant 20°C, natural non-direct illumination), where larvae remained for 72 h before being tested for the perception of vibrational cues. At this step, larvae were released from heat stress conditions and were allowed to acclimate to new thermally neutral conditions mentioned above. Perception testing was performed according to previous methods (Miler et al. 2018). We tested the larvae for vibration response at 6 predefined distances from the edge of their traps (15, 12, 9, 6, 3, and 0 cm), with a 10-min interval between the different testing distances. Vibrational cues involved the delivery of sand (1 mL) through a funnel with an attached plastic pipette tip from a standardized height (5 cm). The larvae remained immobile on the bottom of the trap most of the time but showed an array of reactions after sensing the vibrations delivered in the described way, from submerging in the substrate, through visibly protruding mandibles to tossing sand. The testing of each larva began at the longest distance (15 cm) and proceeded incrementally to the shortest distance (0 cm), and we noted the distance from the trap at which the larva showed any response to the vibrational cue. Following earlier recommendations (Kardish et al. 2015), we conducted the tests blind, with coded information about the regime from which a larva originated.

### Statistical analysis

We performed statistical analyses using the statistical programming language R (R Core Team 2020). We compared the mortality of antlions using a generalized linear model with binomial distribution, logit link function, and 2 fixed factors, the heat stress regime (mild vs. harsh) and initial body mass, and their interaction. We used a negative binomial generalized linear model with a log link function to compare the number of days until molting occurred among individuals who remained alive. In the model, we included 2 fixed factors, the heat stress regime (mild vs. harsh) and initial body mass, and their interaction. We used a general linear model including data only from individuals who remained alive to assess the final body mass. In the model, we included 2 fixed factors, the heat stress



**Figure 2.** Number of days until molting occurred under the heat stress regimes (mild, 30°C, or harsh, 36°C) in relation to the initial body mass. Lines represent model predictions, with shading indicating estimated 95% confidence intervals.

regime (mild vs. harsh) and initial body mass, and their interaction. In our perception tests, some antlions never reacted to vibrational cues at any distance. We compared the number of responsive and non-responsive individuals in each of the 2 regimes using Fisher's exact test (FET). Then, focusing only on the responsive individuals, we used a generalized linear mixed model with a binomial distribution and logit link function to analyze data obtained from different distances, with the heat stress regime (mild vs. harsh) as a fixed factor and final body mass and distance as 2 numerical covariates. The model also included larval id as a random factor (we had repeated information on the same individuals from different distances).

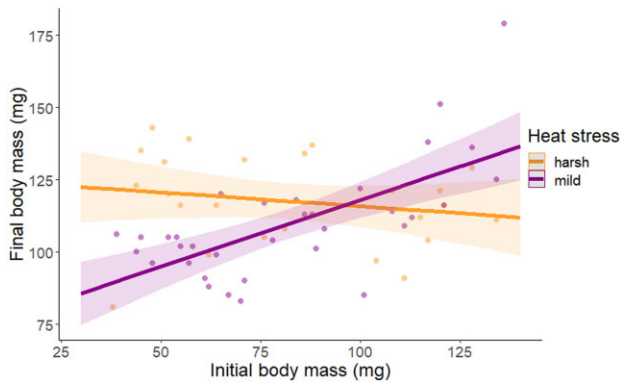
### Results

During exposure to the 2 heat stress regimes, mortality was higher under harsh stress than under mild stress ( $\chi^2 = 4.137$ ,  $P = 0.042$ , Figure 1). The initial mass of larvae was not significant ( $\chi^2 = 0.332$ ,  $P = 0.565$ ), and neither was the interaction between the initial body mass and the heat stress regime ( $\chi^2 = 0.010$ ,  $P = 0.919$ ). Among the individuals who remained alive, the number of days until molting occurred was lower under mild stress than under harsh stress ( $\chi^2 = 32.404$ ,  $P < 0.001$ ). Additionally, we found a significant effect of the initial body mass on molting ( $\chi^2 = 10.352$ ,  $P = 0.001$ ), with larger larvae molting sooner than smaller larvae under both regimes (an interaction between initial body mass and heat stress regime was not significant,  $\chi^2 = 0.367$ ,  $P = 0.545$ ) (Figure 2). For the final body mass measured at the end of our experiment, we found a significant interaction between the initial body mass and the heat stress regime (Table 1 and Figure 3). It appears that following molting, among the initially small individuals, more mass was gained under harsh stress than under mild stress, but the pattern was reversed among the initially large individuals, with the larvae gaining less mass under harsh stress than under mild stress. In fact, some initially large individuals lost mass—and the majority of these larvae originated from the harsh heat stress regime (Figure 3). Our analysis of the perception of vibrational cues showed that 2 out of 24 larvae (originating from harsh heat stress) and 5 out of 34 larvae (originating from mild heat stress) did not respond to the cues, and the proportion of non-responsive individuals did not differ between the 2 regimes (FET yielded  $P = 0.688$ ). When analyzing the data for the larvae that were

**Table 1.** Results of the model for the final body mass of third-instar antlion larvae originating from the mild or harsh heat stress regimes (30°C vs. 36°C)

Model component	<i>F</i>	<i>df</i>	Deviance	Residual deviance	<i>P</i>
Null				19,535.0	
Regime	3.540	1–56	838.1	18,696.9	0.065
Initial body mass	9.042	1–55	2140.7	16,556.2	0.004
Regime × initial body mass	15.929	1–54	3771.3	12,784.9	< 0.001

Notes: The initial body mass represents the measurement taken before the larvae were placed under the regimes as second-instar larvae, while the final body mass represents the measurement taken after molting, when the larvae reached the third-instar stage.



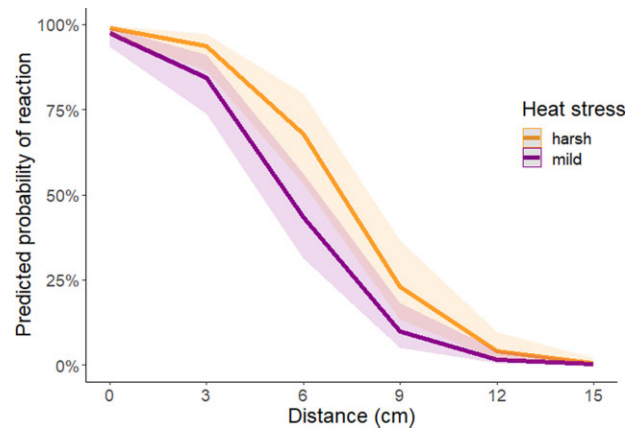
**Figure 3.** Final body mass of larvae originating from the heat stress regimes (mild, 30°C, or harsh, 36°C) in relation to their initial body mass. Lines represent model predictions, with shading indicating estimated 95% confidence intervals.

responsive to the cues, we found that larvae originating from the harsh heat stress regime showed more frequent reactions than those from the mild heat stress regime ( $z = -3.622$ ,  $P < 0.001$ , Figure 4). Generally, all larvae were more responsive to vibrational cues if they were delivered from a relatively short distance ( $z = -5.082$ ,  $P < 0.001$ , Figure 4). Importantly, larvae were consistent in their responses, such that once a larva reacted to the cue at some distance, it always reacted to the cues from shorter distances. Differences in the final body mass among larvae did not explain any significant portion of the variance in response ( $z = 0.036$ ,  $P = 0.971$ ). The interactions included in the model were all not significant (with  $P$  values  $> 0.117$ ).

## Discussion

We found evidence that the 2 thermal regimes used in our experiment imposed different levels of heat stress on developing antlion larvae. Larvae of *M. bore* from the harsh heat stress regime (36°C) had higher mortality (Figure 1), molted later (Figure 2), and, when initially large (but not when initially small), lost body mass (Figure 3) compared with larvae from the mild heat stress regime (30°C). Importantly, our results show that the experience of harsh heat stress resulted in the higher responsiveness of larval antlions to sand vibrations (Figure 4).

Our findings do not agree with our primary scenario that heat stress increases allocation trade-offs, resulting in the handicapped



**Figure 4.** Response to vibrational cues at different distances from the edge of the trap by larvae originating from the heat stress regimes (mild, 30°C, or harsh, 36°C). Lines represent model predictions, with shading indicating estimated 95% confidence intervals.

perceptual ability of the hunting antlion larvae (our “trade-off hypothesis”). It is worth emphasizing that the harsh heat regime decreased larval survival and that the surviving larvae were more responsive to vibrational stimuli compared with the larvae originating from the mild heat stress regime. This shows that we cannot rule out a possibility that heat-induced mortality was particularly high among larvae that, for whatever reason, were less responsive to vibrations. If this was the case, then our combined data on the mortality and behavioral responses suggest that future studies should investigate whether antlions with poorer perceptual ability suffer increased mortality upon acute heat stress. Nevertheless, our results also support the “motivation hypothesis” posing that heat stress “motivated” antlion larvae to respond more to sand vibrations, which would increase the prey-catching capacity and thus reduce the physiological imbalance caused by stressful conditions. This imbalance is suggested by our results on the delayed molting and decreased body mass in the larvae originating from our harsh heat regime. Nevertheless, there is some inconsistency in our results with the “motivation hypothesis”. Our data on body mass indicate that large larvae were likely more food-limited than small larvae, especially under more severe heat stress. So, if our “motivation hypothesis” holds, then we should expect that among larvae exposed to harsh heat stress, large individuals would have higher “motivation” to respond to vibrations compared with small individuals. Against this expectation, we did not find a significant interaction between heat regime and larval body mass in our analysis of antlion responses to sand vibrations. Also, contrasting with “the motivation hypothesis,” when we performed the perception testing, we only sporadically observed reactions that could be clearly connected to prey anticipation, such as opening mandibles or tossing sand. In any case, future experiments will certainly benefit from studying directly the effects of heat stress and food supply (e.g., a food ration in relation to a larval mass) on antlion responsiveness to vibration cues.

It is interesting to note that our results do not agree with earlier evidence that the exposure of second-instar *M. bore* larvae to 40°C each day for a week did not affect mortality and molting in developing larvae (Miler et al. 2020). However, this inconsistency probably reflects different experimental designs. Here, the temperature of 36°C in our harsh heat stress regime constantly affected developing larvae compared with the other study that only temporarily exposed larvae to the temperature of 40°C. It should also be emphasized that

no previous studies have investigated the effect of temperature on antlions' responses to vibration cues. Similarly, studies of other insect taxa have typically focused on the effects of heat stress on survival, fecundity, body size, and mating success (González-Tokman et al. 2020), but not on behavioral processes or perceptual abilities. This emphasizes the need for further studies, including studies devoted to the comparison of the behavior of antlions and wormlions (Diptera: Vermileonidae). These 2 groups provide a fascinating example of convergent evolution as wormlions, like antlions, display a similar hunting strategy that involves using pit traps built in the sand (Miler and Scharf Forthcoming 2021). To our knowledge, the perceptual ability of wormlions has never been studied; therefore, comparing this trait between these 2 convergent groups of insects would be highly insightful.

Overall, our study shows that after prolonged exposure to harsh heat stress, antlion larvae display higher responsiveness to sand vibrations. Local and extreme weather events, such as heat waves, occur increasingly often and become one of the hallmarks of global climate change (Stott 2016), which sets the relevant ecological context for addressing the broader significance of our results. Taking this view, our study helps to consider the potential effects of heat waves on the perception of the environment by antlion larvae. Although identification of such effects is important regardless of the mechanism, we urge future research to better understand causal links between heat stress and responses of antlion larvae to sand vibrations. From a larger perspective, we envision that more research is urgently needed to explore how heat stress shapes behavior in ectotherms. Not surprisingly, climate change is receiving increased attention from biologists, but its impact on behavior has been largely neglected (Sih et al. 2011). Therefore, it looks apparent that addressing links between the thermal environment and behavior will increase our understanding of the biological effects of ongoing global climate change.

## Authors' Contributions

K.M. conceived and designed the study, collected the data, performed the statistical analyses, interpreted the results, and drafted the manuscript. M.C. helped to perform the statistical analyses, interpret the results, and draft the manuscript.

## Data Availability

The datasets generated and analyzed during the current study are available in the Supplementary Excel file.

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## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>

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