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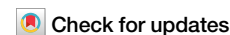
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# The effect of developmental temperature on olfaction in a moth revealed by its interaction with body mass



Thibaut Bagni  , David Siaussat, Thomas Chertemps, Nicolas Montagné, Annick Maria, Annabelle Fuentes, Philippe Couzi & Manuel Massot

There is a growing interest in the effects of climate warming on olfaction, as temperature may affect this essential sense. In insects, the response of the olfactory system to developmental temperature might be mediated by body size or mass because body size and mass are negatively affected by developmental temperature in most ectotherms. We tested this hypothesis of a mass-mediated effect of developmental temperature on olfaction in the moth *Spodoptera littoralis*. We measured the olfactory sensitivity of male to female sex pheromone and five plant odors using electroantennography. We compared males reared at an optimal temperature (25 °C with a daily fluctuation of  $\pm 5$  °C) and at a high temperature ( $33 \pm 5$  °C) close to the upper limit of *S. littoralis*. On average, the olfactory sensitivity of males did not differ between the two developmental temperatures. However, our analyses revealed an interaction between the effects of developmental temperature and body mass on the detection of the six chemicals tested. This interaction is explained by a positive relationship between antennal sensitivity and body mass observed only with the high developmental temperature. Our results show that the effect of developmental temperature may not be detected when organism size is ignored.

Temperature is a key factor in ectotherms, as it influences most of their biological processes<sup>1</sup>. Therefore, most physiological functions in ectotherms are expected to respond to the rise of temperature associated with the current climate change, with important consequences at higher biological scales, such as individuals, populations, communities and ecosystems<sup>2</sup>. Chemical communication is a key parameter that has been suggested to be sensitive to climate warming<sup>3,4</sup>, but the relationship between chemical communication and temperature has been surprisingly understudied<sup>5</sup>. Many insect species use olfaction to perceive and interact with their environment, both for intra- and inter-specific cues<sup>6</sup>. In particular, olfactory cues are used to find mates, oviposition sites on suitable host plants, and food<sup>5,6</sup>. In many moth species, females release pheromones to attract males, and males have a large number of highly sensitive sex-pheromone receptor neurons<sup>7</sup>. Males are also sensitive to plant odors to find food sources and the preferred habitats of females<sup>8,9</sup>. Temperature can impact pheromonal communication at different steps, from biosynthesis, emission, dispersal, and detection to behavioral responses<sup>3,4</sup>. For example, temperature may alter the production and composition of pheromones<sup>10</sup>, enzymatic activity<sup>3,5</sup>, pheromone degradation<sup>11</sup>, affinity between odorants and their receptors<sup>12</sup>, and behavioral responses to odorants<sup>13</sup>.

The aim of our study was to test the effect of developmental temperature on the detection of chemical signals by the pest moth *Spodoptera littoralis*. Studies on pest insects are particularly important because the positive relationships between temperature and the metabolic and population growth rates of pest insects are expected to cause more crop production losses with climate warming<sup>14</sup>. We measured the antennal sensitivity of males to the main component of the female sex pheromone and five plant odors using electroantennography (EAG). Experimental males were reared at two different temperatures, contrasting an optimal developmental temperature and a high temperature close to the upper thermal limit of *S. littoralis*<sup>15–17</sup>. We tested the overall effect of developmental temperature on antennal sensitivity, but also a specific effect mediated by the influence of developmental temperature on body mass. The effects of developmental temperature independent of body mass on antennal sensitivity were expected to be a decrease in antennal sensitivity between our optimal and high temperatures because of the detrimental effects of high temperatures in *S. littoralis*<sup>15</sup>. The mass-mediated effect of temperature on antennal sensitivity was predicted based on two general patterns observed in ectotherms. Kingsolver and Huey<sup>18</sup> summarized these patterns as ‘Hotter is

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smaller' and 'Bigger is better'. The 'Hotter is smaller' pattern describes the negative relationship between developmental temperature and adult size. This relationship is known as the temperature-size rule which David Atkinson<sup>19</sup> found in 83% of studies on ectotherms, and it has been observed in *S. littoralis*<sup>16,17</sup>. Body size and mass have also been identified as major targets of climate warming effects, with most resulting in size reduction<sup>20,21</sup>. The second general pattern, 'Bigger is better', illustrates that larger individuals tend to perform better. Based on the 'Hotter is smaller' and 'Bigger is better' patterns, the expected mass-mediated effect is that the high temperature will produce smaller males than the optimal temperature, and that these small males will be of poorer quality with a lower antennal sensitivity. Furthermore, a specific cause of the mass-mediated effect of developmental temperature on antennal sensitivity is that the number of sensory neurons is usually positively correlated with insect body size<sup>22–26</sup>.

To our knowledge, only three studies have investigated the effect of temperature on odorant sensitivity using EAG. In *Drosophila melanogaster*, Martin et al.<sup>27</sup> showed that odorant detection decreased after a cold treatment (flies reared at 24 °C then transferred to 15 °C for 48 h) and increased after a hot treatment (flies reared at 21 °C then transferred to 30 °C for 48 h). In the moth *Caloptilia fraxinella*, Lemmen and Evenden<sup>28</sup> tested the influence of temperature and photoregime on male sensitivity to the pheromone. The variation in EAG responses depended only on photoregime. In the mosquito *Aedes aegypti*, Lahondère et al.<sup>29</sup> found that the detection of odorants differed between ambient temperatures (responses at 25 °C differed from responses at 20 and 30 °C in an overall analysis of seven odorants), with a trend toward an optimal EAG response at 25 °C for some odorants (octenol, nonanol, hexanol, benzaldehyde, ethanol). Surprisingly, only one study investigated the relationship between EAG responses and individual size at the intraspecific level. Relationships between EAG responses and interspecific variation in body size may result from causes independent of species size, such as morphology of antennae, density of antennal olfactory sensilla, and physiological mechanisms. In the eusocial bumblebee *Bombus terrestris*, Spaethe et al.<sup>22</sup> showed that the antennae of larger workers had higher EAG responses than those of smaller workers. A similar result, based on a behavioral test, showed a positive relationship between body size and recognition of non nestmates in the eusocial bee *Tetragonisca angustula*<sup>26</sup>. Based on this evidence of positive correlations between the size of individuals and the sensitivity of their olfactory system, we believe that the effect of developmental temperature on body size and mass can impact olfactory detection. We tested this hypothesis on the cotton leafworm *S. littoralis*, a major crop pest from North Africa that is now present in all of Africa, southern Europe and the Middle East<sup>30</sup>. We have a good knowledge of its thermal biology<sup>15–17,31,32</sup> and its olfactory system<sup>33–35</sup>, but no study has investigated the effect of temperature on olfactory detection.

## Results

### Test of the overall effect of developmental temperature on EAG responses

EAG responses increased with increasing doses of the main pheromone compound and plant odorants (Fig. 1). EAG responses to all doses tested were significantly higher than the response to the control, except for the lowest dose of the pheromone compound ( $p = 0.47$ ), benzyl alcohol ( $p = 0.63$ ) and linalool ( $p = 0.58$ ). Regardless of the dose, EAG responses to the pheromone compound and plant odors were not affected by developmental temperature (Fig. 1,  $p > 0.10$  in all tests performed for each dose of each chemical).

### Test of the mass-mediated effect of temperature on EAG responses

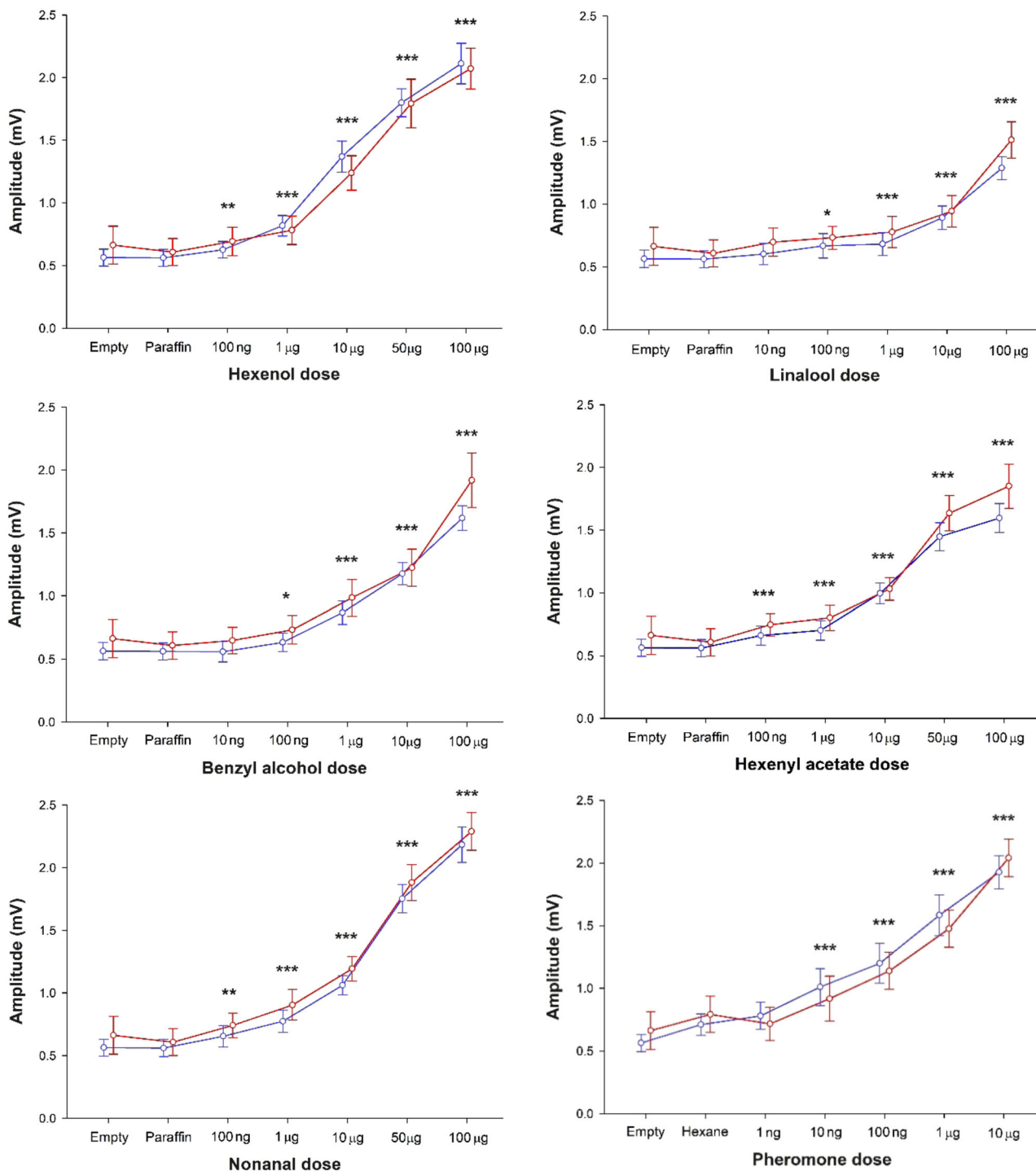
Body mass decreased with increasing developmental temperature ( $t_{114} = -7.8$ ,  $p < 0.001$ ), as expected from the temperature-size rule<sup>18</sup>. Males were larger at 25 °C than at 33 °C (Fig. 2a). Moreover, the male antenna was longer at 25 °C than at 33 °C (Fig. 2b), as antenna size was positively related to body mass ( $F_{1,88} = 26.2$ ,  $p < 0.001$ ) and negatively related to temperature ( $F_{1,88} = 69.4$ ,  $p < 0.001$ ). The temperature effects on body mass and antenna

size open the possibility of a mass-mediated effect of temperature on antennal sensitivity. Male EAG responses to the six chemicals tested were dependent on the interaction between temperature and body mass (significant interactions in 26 out of the 30 tests reported in Figs. 3 and 4). The temperature-body mass interaction was explained by a positive relationship between EAG response and body mass observed only in males reared at 33 °C, as supported by the 23 significant relationships shown in Figs. 3 and 4. At 33 °C, the smallest males had a lower antennal sensitivity than the largest males. We found only two significant relationships out of 30 tests in males reared at 25 °C, a proportion of 6.7% close to the 5% of tests expected under the null hypothesis of no relationship.

## Discussion

Although temperature and organism size are two key factors influencing many traits and performances of species, they are usually studied separately<sup>36</sup>. In particular, to our knowledge, no study on olfactory detection has tested the simultaneous and possibly combined effects of temperature and organism size. In our study, we predicted a reduced antennal sensitivity between optimal and high developmental temperatures because of detrimental effects of high temperatures and/or a mass-mediated effect with high temperatures producing smaller individuals. We focused our experiments on 25 and 33 °C because these temperatures best fitted our goal to compare an optimal temperature to a high temperature with a developmental challenge for *S. littoralis* (Supplementary Fig. 1). Studies on the influence of temperature on olfactory communication of pest insects like *S. littoralis* are valuable because pest insects are expected to cause more crop production losses with climate warming<sup>14</sup>, and many insects use olfactory cues for feeding and reproduction<sup>5,6</sup>. The lack of an overall difference in EAG responses between optimal and high developmental temperatures (Fig. 1) is surprising for two reasons. First, the high temperature of  $33 \pm 5$  °C we applied throughout the full developmental cycle of *S. littoralis* has detrimental effects on larval and pupal survival, as well as on mating success and hatching rate of eggs (Supplementary Fig. 1), resulting in a decrease of its multiplication rate<sup>15</sup>. Second, we observed a decrease in male body mass with temperature (Fig. 2a) and a positive relationship between body mass and antennal sensitivity (Figs. 3 and 4), the two conditions expected from the hypothesis of a mass-mediated effect of temperature on antennal sensitivity. The only unexpected result was that the positive relationship between body mass and antennal sensitivity was found only in males reared at the high temperature of 33 °C and not in males reared at the favorable temperature of 25 °C. This difference between developmental temperatures caused an interaction between the effects of temperature and body mass on antennal sensitivity.

Remarkably, the interaction between the effects of temperature and body mass was revealed for all the chemicals tested (Figs. 3 and 4). Similarly, the positive relationship between body mass and antennal sensitivity in males reared at the highest temperature was observed for all chemicals. Because these odorant molecules are detected by different subsets of odorant receptors in *S. littoralis*<sup>35,37</sup>, our observations most likely result from effects on the global antenna functioning rather than on specific olfactory receptor neurons. Moreover, because the males reared at 33 °C were smaller than those reared at 25 °C, the temperature-body mass interaction may indicate that the dependence of antennal sensitivity on body mass differed between the two ranges of male body mass. Such discontinuities (non-linear relationships and thresholds) between individual size and biological responses are common<sup>29</sup>. Therefore, the particularly small males produced at 33 °C (i.e., the smallest of the small males produced at 33 °C) had the lowest olfactory detection, resulting in the positive relationship between body mass and antennal sensitivity only for males reared at 33 °C. The smallest males produced at 33 °C may have fewer chemosensory neurons, resulting in a less efficient olfaction, if the number of sensory neurons correlates with individual size (via a correlation with antenna size) as observed in other insects<sup>22–26</sup>. This hypothesis is supported by the positive relationship between antenna size and body mass, which is reinforced by a negative effect of temperature on antenna size (Fig. 2b). Alternatively, the smallest males



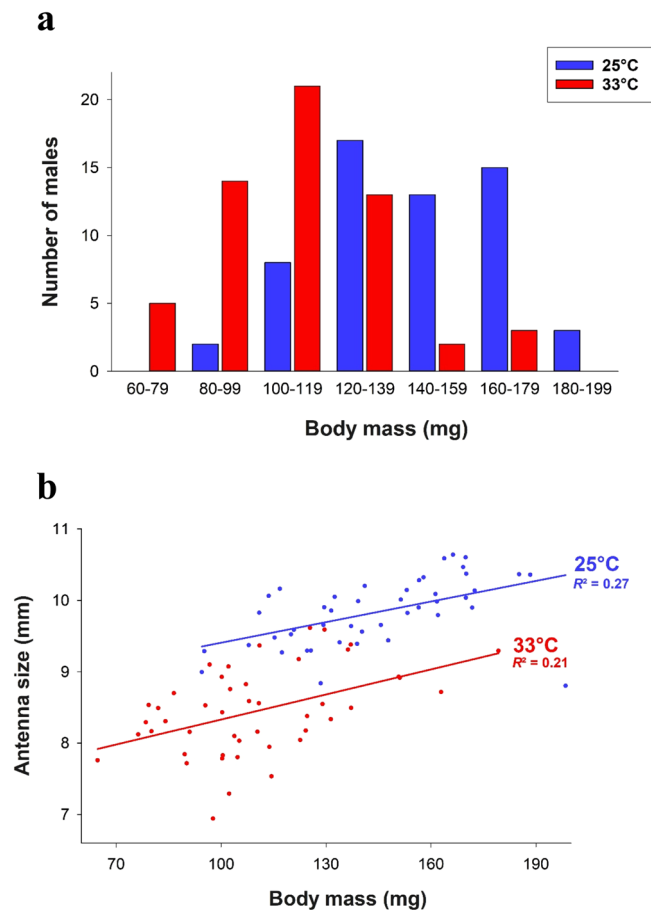
**Fig. 1 | Electroantennography (EAG) responses of males of *S. littoralis* to five plant odors and the main pheromone compound (Z,E)-9,11-14:OAc.** The figure shows mean values  $\pm$  s.e.m. for developmental temperatures of 25 °C (blue circles and lines) and 33 °C (red circles and lines). Each dose was compared to the control stimulation (paraffin for stimulation with plant odorants, and hexane for

pheromone stimulation) with paired t-tests. Significant *p*-values are reported: \**p* < 0.05, \*\**p* < 0.01, and \*\*\**p* < 0.001. The temperature effect between 25 and 33 °C tested for each dose of plant odorants and pheromone, as well as for controls, was always non-significant with *p* > 0.10.

produced at high temperature might have experienced a detrimental effect on the development of their chemosensory system. This hypothesis implies that larger males produced at high temperature avoided this detrimental effect. Larger males might be of better quality (the common ‘Bigger is better’ pattern of Kingsolver and Huey<sup>18</sup>) and better able to maintain their olfactory detection system. The resilience of larger males will be adaptive to avoid a decline in their ability to find females and reproduce. Such adaptive protection of male olfaction at unfavorable temperatures might have

strengthened the positive relationship between body mass and antennal sensitivity in males reared at 33 °C. At this high developmental temperature, an influence of a selection of the more resilient males is also possible because of a higher mortality at 33 °C than 25 °C for larvae and male pupae<sup>15</sup>.

Despite growing interest in the effects of climate change on olfaction in perspective papers<sup>3-5</sup>, few studies have investigated the effects of temperature on odor detection. In addition, the specific context of each study may limit the comparisons across studies. This limitation is illustrated by the



**Fig. 2 | Effect of developmental temperature on body mass and antenna size.** **a** Distribution of body mass of males reared at 25 and 33 °C. **b** Relationship between antenna size and body mass of males reared at 25 and 33 °C.

three published studies of EAG responses as a function of temperature<sup>27–29</sup>. Lemmen and Evenden<sup>28</sup> investigated sex pheromone detection in males of the moth *Caloptilia fraxinella* in the specific context of diapause. They found no difference in EAG responses between cold and favorable temperatures (10 versus 24 °C). In a study on *Drosophila melanogaster*, Martin et al.<sup>27</sup> found a decrease in EAG responses after cold treatment (flies transferred from 24 to 15 °C) and an increase in EAG responses after heat treatment (flies transferred from 21 to 30 °C). This study tested the responses to temperature shifts, which cannot be compared to our results for temperatures applied throughout the life cycle. Lahondère et al.<sup>29</sup> studied the influence of ambient temperature on mosquitoes all reared at 25 °C in *Aedes aegypti*. They found that the EAG responses at the ambient temperature of 25 °C differed from those at 20 and 30 °C. This limitation in comparing studies from different contexts is related to their rarity, and should be addressed with additional studies on the influence of temperature on olfactory detection. Studies with tests on the crossed effects of developmental and ambient temperatures will be particularly interesting. Firstly, to compare the respective importance of delayed and direct effects of temperatures on olfactory detection. Secondly, to investigate the thermal plasticity of olfactory systems such as acclimation responses to face detrimental temperatures.

In addition to the need for further studies on the thermal dependence of the olfactory system, we believe that it is crucial to consider size-mediated effects. Temperature and organism size are key determinants of most biological responses<sup>36</sup>, the negative effect of high developmental temperature on ectotherm size is almost universal<sup>19</sup>, and the impact of warming on body size is a major finding of climate change studies<sup>20,21</sup>. In conclusion, our study on the combined effect of temperature and individual size opens up a

promising avenue of research to explore the effects of climate warming on species' olfactory communication and assess the generality of our results on other ectotherms.

## Methods

### Experimental treatments

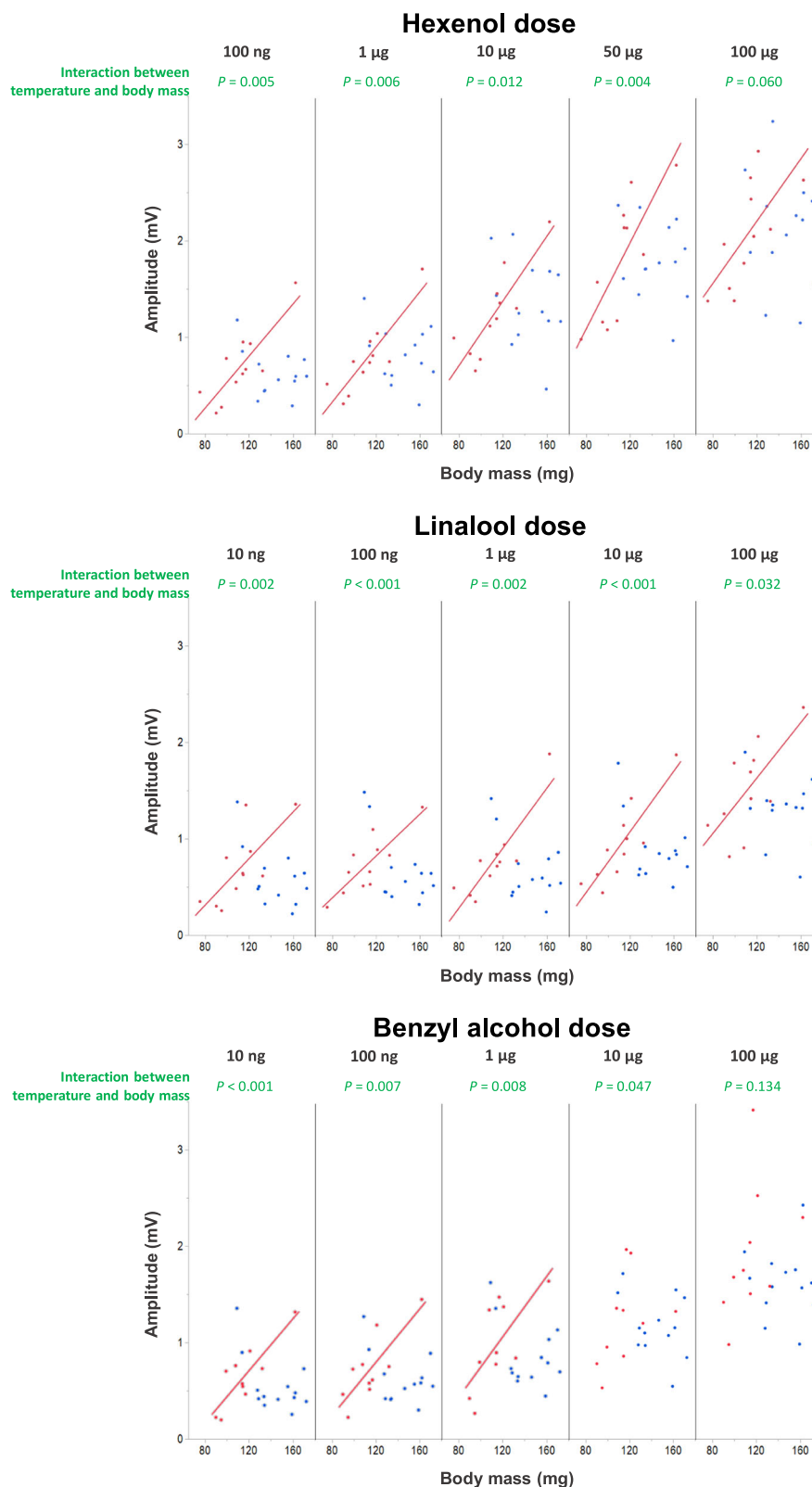
Experimental animals were obtained from a laboratory strain reared on a semi artificial diet<sup>38</sup> at 23 °C, 70% relative humidity, and 16:8 h light/dark cycle. We obtained experimental clutches by mating one male and one female at 23 °C for 24 h in plastic boxes (10 cm of diameter) with sugar water (20 g/L) as food source. To test the temperature effect on the olfactory system of *S. littoralis*, clutches were first separated into two parts to rear them under two different temperatures. The experimental temperatures were 25 and 33 °C, with a daily fluctuation of  $\pm 5$  °C around each temperature (Supplementary Fig. 2). We showed in *S. littoralis*, and more broadly in insects, that ignoring daily fluctuating temperatures commonly leads to underestimate effects of high temperatures<sup>15</sup>. The daily fluctuation of  $\pm 5$  °C is common in natural environments<sup>39</sup> and commonly used in studies on fluctuating thermal regimes<sup>40</sup>. Based on the impact of developmental temperature on fitness in the thermal range we previously investigated in *S. littoralis* with daily fluctuation of  $\pm 5$  °C (Supplementary Fig. 1), we chose temperatures of 25 and 33 °C to compare an optimal temperature to a temperature with a developmental challenge for the olfactory system. The developmental temperature of  $25 \pm 5$  °C is close to the optimal temperature of *S. littoralis* and the temperature of  $33 \pm 5$  °C is close to its upper thermal limit (Supplementary Fig. 1)<sup>15</sup>. At the fourth larval instar, 30 larvae were randomly selected to standardize density in the experimental boxes of each clutch-temperature pool. We checked the boxes until to detect pupation, the time when the individuals were sexed. After pupation, males and females were separated into different climatic chambers to prevent males from acclimating their sensory system to the female pheromone. After adult emergence, males were kept 24 h with sugar water before testing their antennal sensitivity to female pheromone and plant odorants. Males were weighed before their electrophysiological recordings. This experiment was performed from January to March 2022. Using the same protocol, the study was complemented with an experiment in May 2023 to obtain data on the relationship between antenna size and body mass in adult males reared at 25 and 33 °C (with a daily fluctuation of  $\pm 5$  °C). Indeed, antenna size might be a relevant parameter to mediate a relationship between individual size and antennal sensitivity to odors<sup>21</sup>. Antennae were cut at their base, photographed and measured using the software ImageJ<sup>41</sup>. We measured the size of the two antennae of males and used their mean value ( $r = 0.98$ ,  $n = 91$  males, and  $p < 0.001$  for the correlation between the size of the two antennae).

### Chemicals

The male response to female pheromone was tested with the main pheromone compound (Z,E)-9,11-14:OAc of *S. littoralis* and five plant odorants of different chemical classes (benzyl alcohol, ( $\pm$ )-linalool, (Z)-3-hexenol, nonanal, and (Z)3-hexenyl acetate) (Supplementary Table 1). We tested five doses for each of these chemicals, ranging from 1 ng to 10  $\mu$ g for (Z,E)-9,11-14:OAc and from 10 or 100 ng to 100  $\mu$ g for plant odorants. Plant odorants were selected because previous studies on *S. littoralis* have shown that they induced robust EAG responses<sup>42–44</sup>. The pheromone compound (Z,E)-9,11-14:OAc was diluted in hexane and the plants odorants in paraffin oil, two solvents that do not induce EAG responses except a mechanic one due to the pressure of air pulses during recordings. We used cartridges (glass Pasteur pipettes) with odorants to stimulate the animals. As recordings were performed over several days, new cartridges were prepared each day. Ten  $\mu$ L of solution was deposited on a filter paper in each cartridge with odorants. Control cartridges contained only 10  $\mu$ L of hexane or paraffin oil on the filter paper. We also used an 'empty' cartridge containing only a filter paper to normalize the mechanic response due to the air pulses during recordings and to check our control cartridges.



**Fig. 3 | EAG responses to hexenol, linalool and benzyl alcohol as a function of male body mass.** Responses in blue and red are for males reared at 25 °C and 33 °C, respectively. The figure shows only significant relationships at  $p < 0.05$ . Tests of the interaction between temperature and body mass on EAG responses are shown in green.



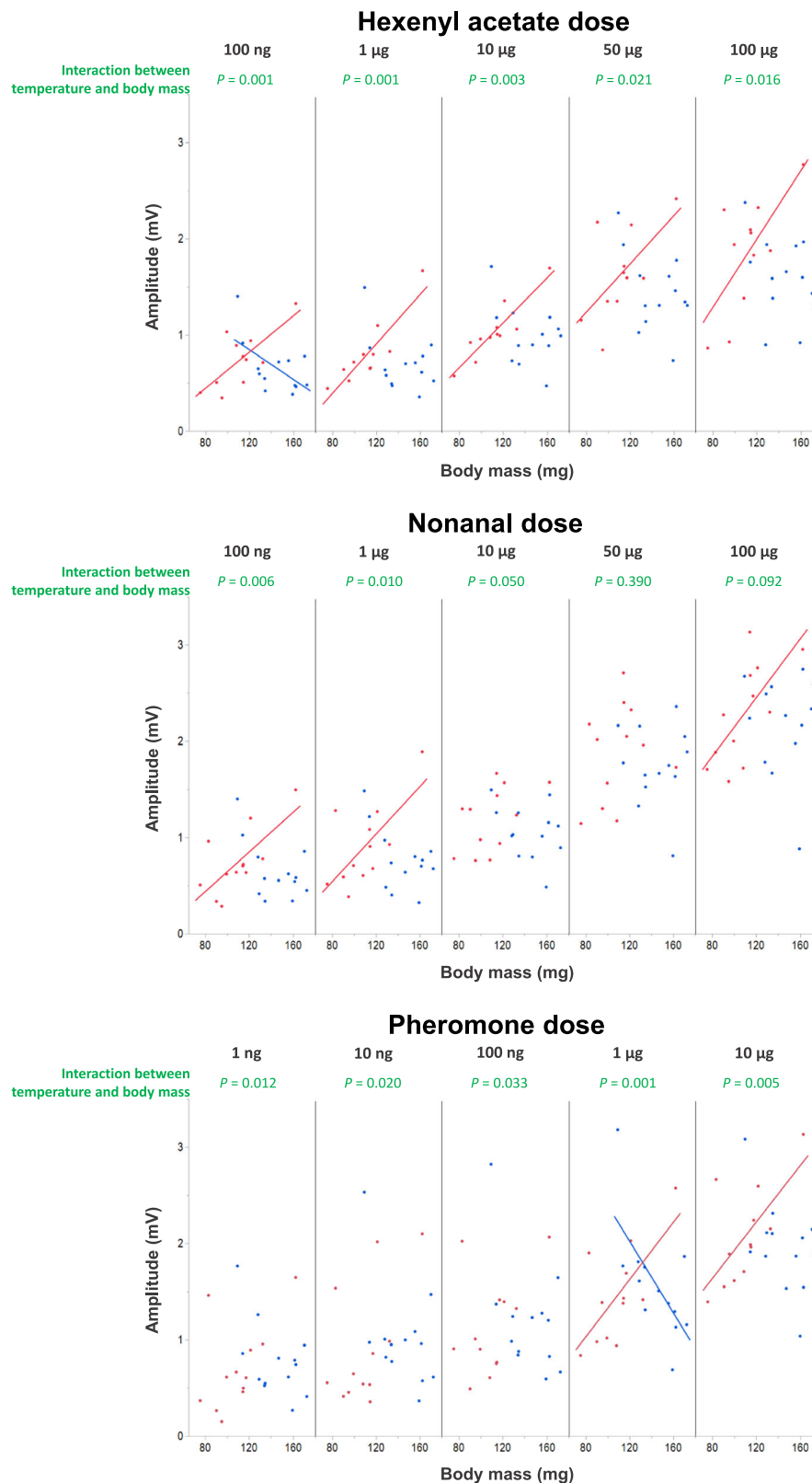
### Electrophysiology recordings

Antennal responses to odorants were measured by electroantennography (EAG) at ambient temperature (mean  $\pm$  SD = 23.1  $\pm$  1.0 °C). EAG recordings were performed during a period of four hours in the middle of the scotophase (fixed from 12 to 20 h for logistic reasons), using Ringer’s solution (120 mM NaCl, 5 mM KCl, 1 mM CaCl<sub>2</sub>, 4 mM MgCl<sub>2</sub>, and 10 mM HEPES, pH 6.5) filled capillary glass electrodes connected to an

amplifier. Moths were immobilized in Styrofoam holders, the reference electrode was inserted into the eye, and the recording electrode was placed into contact with the tip of the uncut antenna with a drop of SPECTRA 360 conductive gel (Parker Laboratories Inc.)<sup>45</sup>. Recorded signals were amplified (x500) through a low-pass filter at 1 kHz using an EX1 differential amplifier (Dagan, USA) and monitored on a computer using a Digidata 1550 A acquisition board (Molecular Devices)

**Fig. 4 | EAG responses to hexenyl acetate, nonanal and the main pheromone compound (Z,E)-9,11-14:OAc as a function of male body mass.**

Responses in blue and red are for males reared at 25 °C and 33 °C, respectively. The figure shows only significant relationships at  $p < 0.05$ . Tests of the interaction between temperature and body mass on EAG responses are shown in green.



controlled by Clampex 10 software (Molecular Devices). A 2 litre per min (LPM) constant air flow was blown over the antenna. The pulse of the stimulus, a 0.5 s air puff at 0.5 LPM, was controlled with a computer-activated electric valve. Each animal was tested with all doses of all odorants, with one minute of recovery time between stimuli. After offline low-pass filtering (50 Hz, Gaussian filter), the maximum depolarization amplitude during odorant stimulation was measured using Clampfit

software (Molecular Devices). The order of presentation of odorants was randomized.

#### Statistics and reproducibility

We obtained measurements of antennae sensitivity in 13 males reared at 25 °C and 12 males reared at 33 °C. EAG responses were log-transformed to satisfy the normality and homoscedasticity assumptions in our analyses. We

used paired t-tests to compare the EAG responses to chemicals with those to the control stimulus (hexane for pheromonal stimulus, paraffin for stimulus with plant odors). Student's *t* test was used to test the effect of temperature (25 versus 33 °C) at each dose of all chemicals and controls (hexane, paraffin and empty cartridge), except for one Wilcoxon test used for the highest dose of 100 µg of nonanal as the normality of the EAG responses was not satisfied even after log-transforming the values. To investigate the mass-mediated effect of temperature, we performed covariance analyses with EAG response as the dependent variable and temperature, body mass and their interaction as factors. A covariance analysis was also used to test the relationship between antenna size and male body mass, with temperature, body mass and their interaction as factors. Analyses were carried out with JMP software (JMP Pro 15, SAS Institute Inc., Cary, NC), and all our tests were two-sided.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data collected during this study are archived in the FigShare data repository<sup>46</sup> <https://doi.org/10.6084/m9.figshare.25923037.v1>.

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### Author contributions

T.B.: conceptualization, investigation, validation, formal analysis, writing – original draft; D.S.: conceptualization, writing – review & editing; T.C.: methodology, writing – review & editing; N.M.: methodology, writing – review & editing; Annick Maria: methodology, resources; A.F.: methodology, resources; P.C.: methodology, resources; M.M.: conceptualization, validation, formal analysis, funding acquisition, writing – review & editing, supervision.

### Competing interests

The authors declare no competing interests.

### Additional information

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