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What does heat tell a mosquito? Characterization of the orientation behaviour of *Aedes aegypti* towards heat sources

Paula F. Zermoglio[a,b,*], Eddy Robuchon[b], María Soledad Leonardi[c], Fabrice Chandre[d], Claudio R. Lazzari[b]

[a] *Departamento de Ecología, Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina*
[b] *Institut de Recherche sur la Biologie de l'Insecte, UMR CNRS 7261, Université François Rabelais, Tours, France*
[c] *Instituto de Biología de Organismos Marinos, Centro Nacional Patagónico (CENPAT-CONICET), Puerto Madryn, Argentina*
[d] *MIVEGEC, IRD 224-CNRS 5290-UM1-UM2, Laboratoire de lutte contre les Insectes Nuisibles (LIN), Montpellier, France*

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ABSTRACT

The use of heat as a cue for the orientation of haematophagous insects towards hot-blooded hosts has been acknowledged for many decades. In mosquitoes, thermoreception has been studied at the molecular, physiological and behavioural levels, and the response to heat has been evaluated in multimodal contexts. However, a direct characterization of how these insects evaluate thermal sources is still lacking. In this study we characterize *Aedes aegypti* thermal orientation using a simple dual choice paradigm, providing direct evidence on how different attributes of heat sources affect their choice. We found that female mosquitoes, but not males, are able to discriminate among heat sources that are at ambient, host-range and deleterious temperatures when no other stimuli are present, eliciting a positive response towards host-range and an avoidance response towards deleterious temperatures. We also tested the preference of females according to the size and position of the sources. We found that females do not discriminate between heat sources of different sizes, but actively orientate towards closer sources at host temperature. Furthermore, we show that females cannot use IR radiation as an orientation cue. Orientation towards a host involves the integration of cues of different nature in distinct phases of the orientation. Although such integration might be decisive for successful encounter of the host, we show that heat alone is sufficient to elicit orientation behaviour. We discuss the performance of mosquitoes' thermal behaviour compared to other blood-sucking insects.

1. Introduction

The survival and reproduction of haematophagous insects depend on their ability to find hosts. Detection of and orientation towards hosts has been extensively studied for decades, pursuing feasible means of controlling their populations and reducing the prevalence of vector-borne diseases. Although the cues that these insects are able to detect before encountering the host can be of chemical or physical nature, particular emphasis has been made on the physiological and behavioural responses to odorants (Zwiebel and Takken, 2004).

Orientation following physical cues, such as thermal or visual ones, has been much less studied than chemical orientation, and has generally been approached from multimodal perspectives (i.e., where more than one type of stimulus is tested simultaneously; McMeniman et al., 2014; van Breugel et al., 2015). Particularly respecting heat detection and the use of thermal information when seeking for food,

only a few species have been studied in detail, in spite of the relevance these aspects have for the haematophagous way of life. For instance, up to date, thermal sense has only been extensively investigated in triatomine bugs. Triatomines exhibit the highest thermal sensitivity reported in animals to date, they are able to detect infrared radiation, to evaluate the temperature of distant sources, and to respond specifically to objects at the temperature of a host, if they are warmer than the surrounding environment (Fresquet and Lazzari, 2011; Lazzari, 2009; Lazzari and Núñez, 1989; Schmitz et al., 2000). Thermal receptors have been identified on the antennae of these insects (Insausti et al., 1999; Lazzari and Wicklein, 1994; Zopf et al., 2014a,b), and their implication not only in host-detection, but also in other behaviours, has been established (Ferreira et al., 2007; Lorenzo Figueiras et al., 2013; Schilman and Lazzari, 2004; Vinauger et al., 2013).

In mosquitoes, the thermal sense has been characterized only partially, and knowledge in the matter has remained roughly constant

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for the last 60 years, until only recently, when community interest for this topic was resumed. Early studies have shown that mosquitoes are attracted to heat within the host temperature range (Howlett, 1910; Peterson and Brown, 1951), and that their responsiveness to heat depends on the environmental temperature and is state-dependant (Thomson, 1938). Two types of thermal receptors have been identified on *Aedes aegypti* antennae, both in females and males (Davis and Sokolove, 1975; McIver and Siemicki, 1979), and putative thermo-sensilla were also found in other mosquito species (e.g., *Anopheles stephensi*, Boo, 1980). In more recent molecular and physiological studies, TRP (transient receptor potential) genes potentially related to thermal sensation have been identified in *An. gambiae* and *Ae. aegypti* (Bohbot et al., 2014; Corfas and Vosshall, 2015; Wang et al., 2009).

From a behavioural point of view, the role of thermal cues has also been analysed in multimodal contexts at different scales. Healy et al. (2002) found that in *An. gambiae* landing rates on a surface containing an odorant stimulus were significantly higher when the temperature was within the host range (34° ± 2 °C). Similarly, Olanga et al. (2010) showed in the same species that, at a short range, the response to odours was augmented by the presence of heat and moisture. Also, Spitzen et al. (2013) demonstrated that, although heat alone did not affect mosquitoes' flight patterns, the combination of heat and odour cues resulted in longer flights, increased flight speed and more landings on the source. Concordantly, in *Ae. aegypti*, McMeniman et al. (2014) observed that, although CO_2 seems to be a main driving factor for orientation, attraction to hosts results from the integration of CO_2, hosts odours and heat cues. Most recent evidence suggests that the distinct cues would be used differently upon the proximity of the source, and that heat would play an important role at short distances, particularly on mosquitoes landing (van Breugel et al., 2015). All this evidence supports the notion that heat constitutes one of the cues that, at least in conjunction with other modalities, participates in mosquitoes' host location.

Even though it is broadly accepted that heat is involved in host-seeking in mosquitoes, the type of information they can obtain about a potential host using their thermal sense remains to be analysed. The aim of this study was to investigate orientation of mosquitoes towards heat sources in the absence of other host cues and to characterize their ability to discriminate between heat sources differing in temperature, size and distance, the three variables involved in thermal energy exchange. We analysed, in addition, whether mosquitos are able to use the radiant heat (i.e., infrared radiation) emitted by an object to localize it in space, and whether male individuals respond to heat sources. We chose *Ae. aegypti* as a model because: 1) this species is widely utilized to explore basic aspect of the biology of mosquitoes; and 2) it is the main vector of yellow fever, dengue, Chikungunya and Zika viruses, and other pathogens in tropical and subtropical regions, which renders it a species of great sanitary importance.

2. Material and methods

2.1. Insect rearing

Ae. aegypti eggs of the Bora strain (sensitive to insecticides) were obtained from the Laboratoire des Insectes Nuisibles, Institut de Recherche pour le Développement (IRD, Montpellier, France). Insects were reared at 25° ± 1 °C, 70 ± 5% relative humidity, 12:12 light/dark regime, in containers with dechlorinated water, supplemented with ascorbic acid for egg hatching and with food *ad libitum* until adult emergence. Adults were kept in 30 × 30 × 30 cm mesh cages supplied with wet cotton patches soaked with 10% sucrose solution, and deprived of blood meals.

2.2. Experimental setting

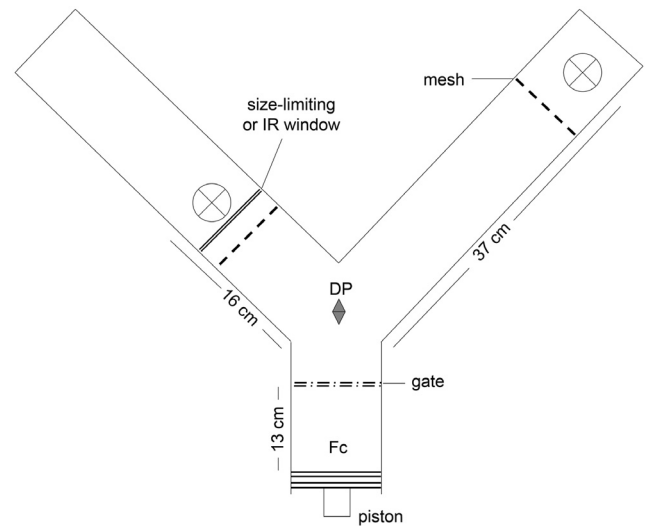For testing the orientation of mosquitoes towards different heat

Fig. 1. Experimental device. Acrylic Y-tube (13 cm diam.). A familiarization chamber (Fc), closed in its extreme by a removable piston, is separated from the testing zone by means of an acrylic gate bearing a mesh window (6.5 cm diameter). The centre of the Y-tube, placed 4 cm from the gate, was set as the decision point (DP). The extremes of the Y arms are closed by a mesh, after which heat sources (⊗) were suspended inside the tube either at a close or at a far distance.

sources we used an acrylic Y-tube (13 cm diameter, Fig. 1). A familiarization chamber, closed in its extreme by a removable piston, was separated from the testing zone by means of an acrylic gate bearing a mesh window (6.5 cm diameter), placed at 13 cm from the extreme of the tube. The centre of the Y-tube, placed 4 cm from the gate, was set as the decision point. The extremes of the Y arms were closed by a mesh, after which heat sources were suspended inside the tube either at a close or at a far distance from the meshes (see below). Heat sources consisted of low-power light bulbs painted with opaque black acrylic paint that were connected to a voltage regulator and to digital thermostats (ENDA Industrial Electronics ETC 1311-FE 230VAC). This setup allows accurately setting desired temperatures, but without emission of any visible light. The temperature controllers measure the temperature on the surface of each bulb by means of thermocouples and regulate the electrical input, hence keeping the surface temperature on each bulb constant and independent of the other. In order to simulate a smaller source, we placed a bubble foil reflective insulation disc with a 3 cm diameter hole between the bulbs and the mesh that delimits the testing zone. To test if the insects can detect IR radiation, an IR window (Edmund Optics, France, Ref: 32-808) was placed between the thermal source and the mesh, which only allows IR radiation to pass through but not establishing a temperature gradient or convection currents inside the maze.

2.3. Experiments

Mosquitoes were presented with heat sources that differed in temperature (ambient: 25 °C, host range: 34 °C, or deleterious: 50 °C), placing distance (near, 16 cm 19.5° solid angle, or far, 37 cm 8.5° solid angle from the decision point, DP) and/or size (large 23.76 cm² or small 7.07 cm²; solid angles 19.5° and 10.7° at 37 cm and 8.5° and 4.6° at 16 cm). The decision point was set in the centre of the Y-tube, 4 cm away from the gate. Also, in order to determine orientation towards radiant heat, they were presented with stimuli in the form of IR radiation only.

In each experiment we individually subjected 40 insects to dual choices. Replicas were carried on alternating the sides of the Y-tube in which the stimuli were presented (left and right) and on alternating times of the day. For instance, half of the experimental trials of a given condition were run in morning hours and the other half in the
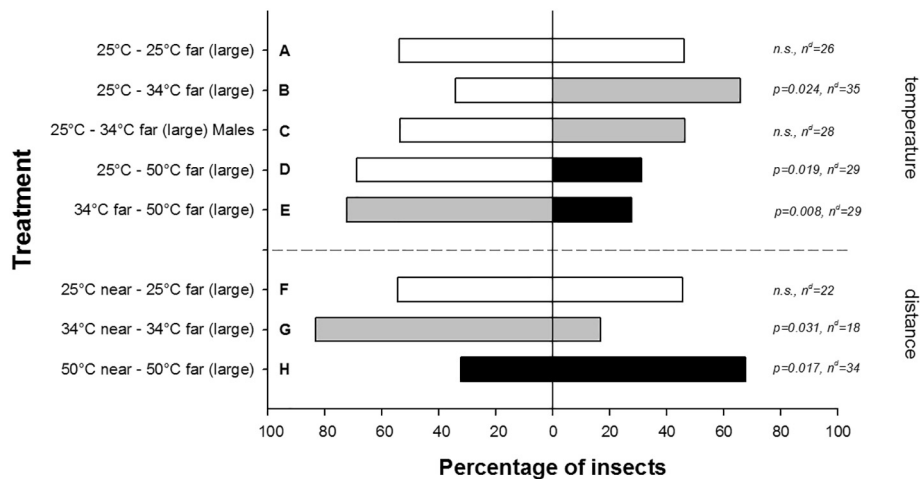
Fig. 2. Orientation of *Ae. aegypti* towards heat sources in dual-choice assays. A–E: Orientation towards equal-size, equal distance thermal stimuli. F–H: Orientation towards equal size, different distance thermal stimuli: equal temperature sources. White bars correspond to ambient temperature, grey bars to 34 °C and black bars to 50 °C. Indicated are the number of deciding individuals (n^d) per treatment of total tested n = 40; and the p values, the significance level corresponds to the analysis of the election of choosing insects (not including non-deciding bugs), performed by means of binomial tests. n.s.: not statistically significant.

afternoon, and this in a side-balanced way. For example, when sources at 25 °C and 34 °C were tested, 10 trials were run during morning hours with the 34 °C source on the right, and other 10 on the left, and this was repeated during the afternoon. This method allows controlling for potential differences between both arms of the Y-tube. Also, the rationale behind this procedure is that this species displays a bimodal spontaneous activity during the day hours with a trough at noon (Jones, 1981). No differences were found between the responses of insects tested in the morning and in the afternoon, and hence all mosquitoes of each treatment were considered together. Also, in order to control for potential differences in the temperature that insects are exposed to at the decision point, we measured the temperature at DP under each experimental condition.

2.3.1. Orientation towards equal-size, equal distance thermal sources

Female mosquitoes were tested in 25 °C vs 25 °C (control), 25 °C vs 34 °C, 25 °C vs 50 °C, and 34 °C vs 50 °C trials. Additionally, males were tested in 25 °C vs 34 °C trials. In all cases, extreme Y-tube meshes were placed 33 cm from the decision point and large heat sources were placed at a far distance.

2.3.2. Orientation towards equal-size, different distance thermal sources

Female mosquitoes were tested in 25 °C far vs 25 °C near (control), 34 °C far vs 34 °C near, 50 °C far vs 50 °C near, 34 °C far vs 50 °C near and 34 °C near vs 50 °C far trials. In all cases, extreme Y-tube meshes were placed 12 cm from the decision point and large heat sources were placed either far or near from it, according to the experiment.

2.3.3. Orientation towards equal distance, different size thermal sources

Females were tested in 34 °C large vs 34 °C small and in 50 °C large vs 50 °C small trials. Experiments were carried out with both heat sources placed near and repeated with both sources placed far.

2.3.4. Orientation in the absence of temperature air-gradients

Females were tested in 25 °C vs 34 °C trials using an IR window placed in front of the heat source and between it and the extreme Y-tube arm mesh, which only allows passing of infrared radiation. Both heat sources were large and placed at the far distance from the decision point with extreme Y-tube meshes placed at 12 cm from it.

Insects were individually released in the familiarization chamber, where they remained 2 min, after which the gate was opened, allowing the mosquito to leave the chamber. We registered the side of the Y-tube chosen by the insect in each treatment. The choice is, in most cases, nearly instantaneous, but in order to account for some individuals that

take longer to choose, we set a maximum experimentation time of 5 min per individual. We considered that an individual made a choice when it crossed a line set at 6 cm from the decision point in either direction of the Y-tube. Each insect was used only once and discarded afterwards. Data for each experiment were analysed by means of exact binomial tests in R (R Core Team, 2015). For this, the number of insects choosing one arm or the other of the Y-maze was counted over the total number of individuals that made a choice in each trial (i.e., leaving out those that did not choose). Proportions were then compared against an expected random distribution, where 50% of the individuals are expected to choose each side. The number of individuals that did not make a choice in each experiment was compared against that of the control (25 °C vs 25 °C far sources) by means of the Pearson Chi-square test (Yates correction was not applied because there were no low data values).

3. Results

3.1. The choice between thermal sources

Temperature remained fairly constant at the decision point, regardless of the treatment (maximum variation = 0.6 °C). Maximum temperature increase at the decision point with respect to ambient temperature, was found when two sources at 50 °C were placed at a close distance (1.3 °C, insects not subjected to this treatment). All insects tested that showed orientation performed direct flights towards the heat sources, landing directly on the corresponding mesh, and not exhibiting any switch in sides once they had initiated flight.

Experiments revealed that *Ae. aegypti* females are capable of orienting towards a heat source which temperature resembles that of a host when the temperature of the source was the only variable of choice. Two sources at room temperature did not elicit orientation behaviour (Fig. 2A). However, when one of the sources was kept at 34 °C and the other one either at ambient temperature or at 50 °C, mosquitoes significantly chose to approach that at 34 °C (p = 0.0243 and p = 0.008, respectively, Fig. 2B and E). We also found that relatively high temperatures (i.e., 50 °C) elicited an avoidance response when presented against ambient temperature (p = 0.0187, Fig. 2D). Males did not orient towards a heat source within the host's temperature range (p = 0.139, Fig. 2C).

When presented with sources at different distances, when sources were at the host temperature, females chose the arm associated with the closest one (34 °C near vs. far, p = 0.0031, Fig. 2G). Conversely, if sources were at potentially deleterious temperatures, they chose the
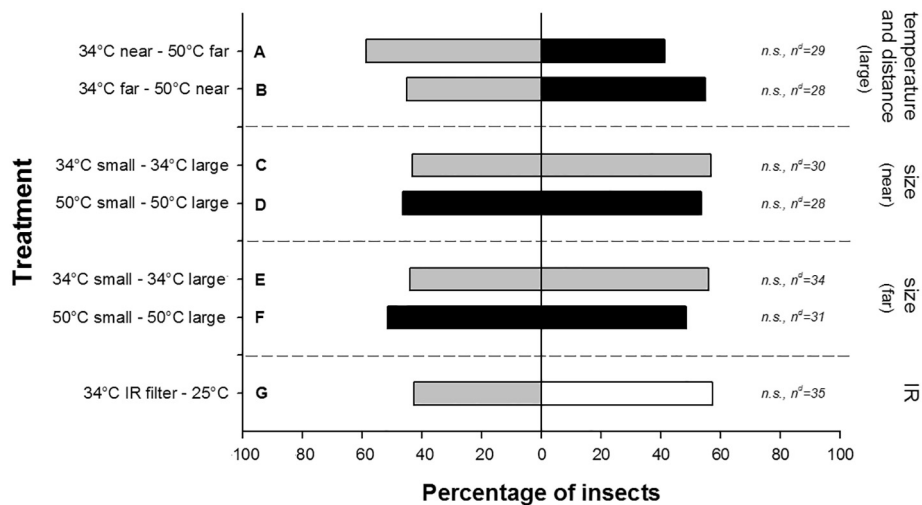
Fig. 3. Orientation of female *Ae. aegypti* towards heat sources in dual-choice assays. A–B: Orientation towards equal-size, different distance and temperature thermal stimuli; C–F: Orientation towards equal distance and temperature, different size thermal stimuli; G: Orientation using radiant heat with an IR window interposed between the source and the insect. White bars correspond to ambient temperature, grey bars to 34 °C and black bars to 50 °C. Indicated are the number of deciding individuals (n^d) per treatment of total tested n = 40. Binomial tests on choosing insects (not including non-deciding bugs) did not reveal differences in any case. n.s.: not statistically significant.

furthest one (50 °C near vs far, p = 0.0167, Fig. 2H). However, when confronted with the co-variation of temperature and distance (i.e., when presented with 34 °C vs 50 °C at different distances), the insects did not discriminate between sources (50 °C near vs. 34 °C far, p = 0.1016; 50 °C far vs. 34 °C near, p = 0.0967; Fig. 3A and B).

Ae. aegypti females did not distinguish between large and small heat sources at either of the two temperatures tested, independently of the distance of the source (34 °C large vs. small near, p = 0.115; 34 °C large vs. small far, p = 0.108; 50 °C large vs. small near, p = 0.1395; 50 °C large vs. small far, p = 0.1399; Fig. 3C–F).

Finally, concerning the detection of radiant heat (IR radiation), when given the choice between a source at ambient temperature versus another at host temperature located behind an IR window, they did not significantly choose one over the other (p = 0.0945, Fig. 3G).

3.2. To choose or not to choose

When the proportion of insects that effectively made a choice was compared against that of the control (no stimulus), we observed that cases in which a large proportion of mosquitoes were responsive were associated with a significant preference for one of the two conditions presented (Table 1). However, the reverse was not true, since we

detected preference in some cases where the amount of responsive insects was lower (e.g., 50 °C far – 34 °C far), and also a high proportion of females making a choice did not necessarily correspond to a significant preference (e.g., 25–34 °C + IR filter). Therefore, the proportion of insects that elicit a response cannot be considered of high informative value on the behaviour of mosquitoes within our experimental paradigm.

4. Discussion

In this study we present a characterization of *Ae. aegypti* responses to heat sources presenting different characteristics (i.e., temperature, distance to and size of the source), as well as nature of the heat exchange (i.e., radiation or conduction). Our results provide a characterization of the behaviour of mosquitoes towards thermal sources in the absence of other host-associated stimuli, an orientation situation that has been relatively disregarded in recent literature.

We found that the orientation towards heat sources is limited to female individuals, which seems not surprising given that host feeding is exclusive of females. It is worth mentioning, however, that thermal receptors have been identified in both females and males in *Ae. aegypti* and in other mosquito species (Boo, 1980; Davis and Sokolove, 1975;

Table 1

Non-deciding *Ae. aegypti* individuals in the different experiments. The proportion of insects making and not making a choice were compared to those obtained in the negative control.

Treatment	# non-deciding individuals	Proportion[1]	χ^2-value	*p*-value	Corresponding Figure
(large) 25–25 °C far[2]	14	0.35	–	–	2A
(large) 25–34 °C far, Females	5	0.125	5.59	0.018[*]	2B
(large) 25–34 °C far, Males	12	0.3	0.23	0.633	2C
(large) 25–50 °C far	11	0.275	0.52	0.469	2D
(large) 34 °C far – 50 °C far	11	0.275	0.52	0.469	2E
(large) 25 °C near – 25 °C far	18	0.45	0.83	0.361	2F
(large) 34 °C near – 34 °C far	4	0.1	7.17	0.007[*]	2G
(large) 50 °C near – 50 °C far	6	0.15	4.27	0.038[*]	2H
(large) 34 °C near – 50 °C far	11	0.275	0.52	0.469	3A
(large) 34 °C far – 50 °C near	12	0.3	0.23	0.633	3B
(near) 34 °C small – 34 °C large	10	0.25	0.95	0.329	3C
(near) 50 °C small – 50 °C large	12	0.3	0.23	0.633	3D
(far) 34 °C small – 34 °C large	6	0.15	4.27	0.038[*]	3E
(far) 50 °C small – 50 °C large	9	0.225	1.53	0.217	3F
(large, far) 34 °C IR filter – 25 °C	5	0.125	5.59	0.018[*]	3G

[1] Total individuals per treatment was n = 40.
[2] Control treatment (expected proportion).
[*] Statistically significant differences (Pearson's Chi-square test).

McIver and Siemicki, 1979). The absence of an oriented response in males suggests that thermoreceptors do not serve orientation to heat sources in the absence of other stimuli. However, it remains to be tested if males are capable of using heat cues in relation to other behaviours, such as thermopreference.

When analysing temperature selection, we found that females actively oriented toward heat sources at temperatures roughly corresponding to that of a host, behaviour that had been suggested by early studies in which heat was presented alone, and more recently observed when heat was combined with other host cues (Healy et al., 2002; Howlett, 1910; Peterson and Brown, 1951; van Breugel et al., 2015). Our observation on the avoidance of higher, deleterious temperatures (50 °C) is in agreement with generalized thermopreference behaviour. In mosquitoes, studies on the avoidance of ambient high temperatures have shown that different species present distinct temperature thresholds, which would allow them to exploit different niches (Brady et al., 2013; Kirby and Lindsay, 2004). In our experiments, we presented sources which temperature was beyond the informed thresholds and thus can be considered as deleterious for these insects.

Our results show that mosquitoes distinguish among sources that are presented at different distances. For instance, they actively oriented towards closer sources when their temperature corresponded to that of a host and avoided a close source at a deleterious temperature. Conversely, differences in the size of the source did not evoke any significant preference. Although the difference in size between sources that we used might not represent differences between potential hosts and other heat sources in nature, our results show that the size of the source did not affect orientation behaviour under our experimental paradigm. Therefore, we can conclude that, of the three variables determining the heat flow between a thermal source and a mosquito, only temperature and distance information, but not the size of the source, seem to be used by *Ae. aegypti* females. We discuss the link between the three variables and their implication for haematophagous way of life below.

When presented with heat sources that varied not only in temperature but also in distance (i.e., two dimensions that the insects seem to evaluate when tested independently), mosquitoes were not able to choose between sources anymore. The same result was obtained when size and temperature, or size and distance were switched simultaneously (Fig. 3).

Although body temperature is the variable that characterises a warm-blooded host and allows mosquitoes to recognise it as such, the physical stimulus received by mosquito antennae is thermal energy. This energy, once absorbed by specialised sensory structures (thermoreceptors) increases the temperature of the receiver, activating specific molecular receptors (e.g., TRPs). Although both the temperature of the host and that of sensory receptors vary, the link between variation in one and the other is not direct, as temperature defines a state but does not constitute a form of exchangeable energy. According to the Stephan-Boltzmann law, the amount of thermal energy reaching an object from another at a higher temperature (which is usually the case between hosts and mosquitoes) depends on three variables: 1) the temperature difference between the objects, 2) the size of the objects (or their emitting area), and 3) the distance between the objects. As a consequence, it can be expected that the simple stimulation of thermoreceptors is not sufficient for the insects to precisely evaluate any of these variables separately, nor to derive the temperature of the object of interest. Instead, to have information on one variable in particular, the insect would need to know, estimate or assume the values of the other two parameters. Some insects, such as kissing-bugs, are able to specifically respond to the temperature of an object, notwithstanding its size or the distance to it (Lazzari, 2009; Lazzari and Núñez, 1989). Hence, they do not just respond to a temperature difference between the object and the background, but specifically to objects which temperature corresponds to that of a host (Fresquet and Lazzari, 2011).

Our results show that mosquitoes are only able to distinguish

between two sources at different temperature if they are placed at the same distance, or between two sources at the same temperature located at different distances. Other combinations of heat sources, or simultaneous variation in more than one parameter, did not allow mosquitoes to choose the appropriate source (i.e., the closest, the biggest or the one at the temperature of a host).

According to physics, heat exchange can take place by three mechanisms: conduction, convection and radiation. Heat conduction establishes a temperature gradient in the air between the source and the insects. Convection constitutes a movement of air induced by the difference in the density of the air in direct contact with the heat source and the further, cooler environment. Finally, infrared radiation is emitted by any object which temperature is above 0 K (absolute zero). The implications for the perception of a heat source of the occurrence of heat exchange by each of these mechanisms are different and highly relevant for haematophagous (see Lazzari, 2009). Whereas air-temperature gradients provide "a path to follow", they are easily disrupted by air turbulence. Convection establishes ascending air currents that may transport odours, carbon dioxide and water-vapour, providing access to multimodal cues. Their ascending nature, however, make air currents exploitable only when the insect approaches the host from above. Finally, infrared radiation is not affected by turbulence or the relative position of the receiver. In addition, it scatters radially, providing more precise spatial information than conduction or convection.

Despite its advantages, the ability to detect and use IR radiation for locating resources seems to be a rare feature in the animal kingdom. This capacity has been well established in some snakes, which use their IR-sense to find preys (Bullock and Cowles, 1952), and in beetles belonging to the genus *Melanophila* (Coleoptera: Buprestidae), which use it to seek forest fires to colonize (Evans, 1964; Schmitz and Bleckmann, 1997). Among haematophagous insects, the ability to detect IR radiation began to be investigated long time ago (Peterson and Brown, 1951; Wigglesworth and Gillet, 1934), and its occurrence was demonstrated for the first time in kissing-bugs (Lazzari and Núñez, 1989). In this context, we investigated whether mosquitoes use IR radiation as an orientation cue, by performing choice tests interposing an IR window between a heat source and the insect, which allowed the IR radiation of the source to reach the insects but hindered conduction and convection mechanisms. Our results show that mosquitoes did not actively orient towards a source when radiant heat was the only available cue. Although we cannot discard the possibility that mosquitoes detect IR, we show that they do not use heat radiation for orienting. This finding is in agreement with results presented by Gingl et al. (2005), who suggest that IR radiation would not constitute a significant cue in host location. Also, it is consistent with observations made by other authors, who suggested that radiant heat might not be a decisive cue for host-seeking in *Aedes* mosquitoes but that, instead, convection currents would be what modulates their behaviour (Khan et al., 1968; Peterson and Brown, 1951). The role of convection currents has also been tested in other mosquito species with similar results (Dekker et al., 1998).

Recently, the thermal sense of mosquitoes has been analysed in terms of its molecular bases (Corfas and Vosshall, 2015; Wang et al., 2009) and of its role as a cue in multimodal host-location (Cardé, 2015; McMeniman et al., 2014; Spitzen et al., 2013; van Breugel et al., 2015). These studies shed much light on how heat is perceived and how thermal information is used during host searching. For instance, one important conclusion is that, in a multimodal context, each cue presents a distinct range of action. The present study completes the picture, providing insights on how mosquitoes evaluate warm objects in the context of finding potential hosts.

In summary, our experiments reveal that heat alone can be used as an orientation cue by starved female mosquitoes (i.e., deprived of blood meals), but not by males, and that they are able to discriminate between objects at different temperature, recognizing those resembling a host

solely by their temperature. The experiments also revealed that *Ae. aegypti*, in contrast to triatomine bugs, are not able to solve temperature-size-distance ambiguities of thermal sources, the three variables determining how much thermal energy stimulates thermoreceptors. Given these results, we could hypothesize that the thermal sense of different haematophagous is not organized or developed similarly, although the basis for this comparison remains weak, since only triatomine bugs and mosquitoes have been studied in detail. While bugs are sensitive to IR and use radiant heat to locate a potential host (Lazzari and Núñez, 1989; Schmitz et al., 2000; Zopf et al., 2014a,b), mosquitoes do not use this information (Peterson and Brown, 1951; this study), and the way in which these species acquire and use thermal information seems to be directly related to their biology. Kissing bugs are haematophagous during their whole life and are mostly walking insects (even though adults can perform dispersive flights). They are eclectic blood-feeders, live inside nests and human dwellings, and can approach their hosts from virtually any direction (they can walk on the ground, climb walls and ceilings and approach flying when adults). Therefore, as bugs are able to detect a host from any possible relative position notwithstanding air turbulences or the direction of air currents (host downwind or upwind), using their IR sense represents a selective advantage. Mosquitoes, in turn, except when inside houses, must find their hosts in open areas. This lifestyle would favour the utilization of senses that depend on air currents, performing olfactory-triggered anemotaxis and following convection currents that transport host-volatiles (Cardé, 2015; Khan et al., 1968; Peterson and Brown, 1951; van Breugel et al., 2015), thus rendering heat only one additional cue in a multimodal context.

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