Escape strategy of the cockroach (Gromphadorhina portentosa) to heat and looming stimuli

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Escape strategy of the cockroach (*Gromphadorhina portentosa*)

to heat and looming stimuli

An Honors Program Project Presented to
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by Jiangda Ou

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Abstract

Escape responses to aversive stimuli have been observed in insects, including species of cricket, fly, locust, and cockroach. The goal of this study was to investigate the escape strategy of the Madagascar cockroach, *Gromphadorhina portentosa*. In regard to this species, Erickson and colleagues (2015) showed that electrical stimulation of both cerci and antennae together could generate an escape response. However, in other reports (Olsen and Triblehorn, 2014), it was observed that wind could not elicit the escape response. In this study, *G. portentosa* was stimulated by looming and heat stimuli. A 2.5” black ball approaching at 1 m/s was used to mimic a predator and a laser was used to apply heat stimuli to the cockroach’s tarsi. The results showed that heat stimuli evoked robust turning and translation responses while the looming stimuli evoked small but significant translation but not turning. In conclusion, and in contrast to the literature, Madagascar cockroaches displayed robust escape responses to looming and especially heat stimuli.
**Introduction**

Insects are the most common group of animals on the earth (The IUCN Red List of Threatened Species, 2015), appearing everywhere in our daily life. Since insects can affect our life both positively and negatively (e.g. control the ecological balance, crop pest in agriculture), it is important to better understand their behaviors, such as their escape strategies, in order to prevent their negative effects.

Insects have diverse strategies to escape from their predators, including freezing, fighting and escaping (Domenici *et al.*, 2008, 2009; Card and Dickinson, 2008). For example, some cockroaches can fly away from dangers, spiders can produce silks to help them escape, and water striders can walk on water in order to escape from their terrestrial predators. However, one major strategy for escape is to move in the opposite direction from a stimulus. The basic components of escape behavior included turning, walking, jumping (Tauber and Camhi, 1995; Dupuy *et al.*, 2011) and flying (Fraser, 1977; Card and Dickinson, 2008). In real-world situations, insects employ multiple escape behaviors, which vary among insects such as crickets, a locust, flies, and cockroaches.

*Escape Strategy – Cricket*

Crickets escape from wind (Kanou *et al.*, 1999, 2006, 2014; Gras and Horner, 1992; Horner, 1992; Tauber and Camhi, 1995), touch (Dupuy *et al.*, 2011; Hiraguchi and
Yamaguchi, 2000) and looming objects (Dupuy et al., 2011; Hiraguchi and Yamaguchi, 2000) by turning followed by either walking or jumping. Walking can be continuous Kanou et al. 1999) or progress in bouts and pauses (Gras and Horner, 1992).

The escape rate of crickets to experimental stimuli varies greatly (5% - 95%), and was related to factors such as species (Kanou, 2006), age (Dupuy et al., 2011), speed of stimulus (Kanou et al., 1999, 2006), direction of stimulus (Dupuy et al., 2011) and type of stimulus (Dupuy et al., 2011; Hiraguchi and Yamaguchi, 2000).

The response rate varies across cricket species. Gryllodes sigillaus has a higher response rate (94%), then Gryllus bimaculatus (58%; Kanou et al., 1999, 2006). This difference suggests that species plays an important factor in predicting escape strategies. Age was also a factor. Younger crickets had a higher probability of successfully escaping from threats. Juvenile crickets, Nemobius sylvestris (1st- 3rd instars), had a high response to a looming object (40% - 100%), which was significantly higher than the older crickets (8% - 65%; 7th – 9th instars and adults; Dupuy et al., 2011). The reason younger crickets escape at higher rates may be because they are at greater risk of predation (Dangles et al., 2006a).
The response rate also differed with stimulus direction, stimulus speed and the type of stimulus. The response rate for stimuli approaching from the front, side and back were 18% – 40%, 55% – 100% and 58 – 100%, respectively, showing a significantly higher response rate when the stimulation came from the side rather than from the front (Dupuy et al., 2011).

The response rate was typically higher with higher stimuli speed. When the velocity of air-puff was 3.0 – 3.9 m/sec, the normal adult cricket response rate was 51% – 56%. However, if the velocity of air-puff dropped to 1.5 m/sec, the response rate dramatically decreased to only 6% (Kanou et al., 1999). In G. bimaculatus, the response rate in response to touching was 52%, but increased to about 95% when crickets were stimulated by bending or pinching (Hiraguchi and Yamaguchi, 2000). In another species, Nemobius sylvestris, the response rate to a looming object was only 5 - 52% (Dupuy et al., 2011).

Escape direction varied among cricket species, but all typically escaped in the opposite direction from the stimulus (100° - 170°, e.g. 0°: straight forwards to the stimulus, 180°: directly away from the stimulus, Figure 1). G. bimaculatus, escaped at 162° opposite to air-puff (Kanou, 1999), while G. sigillatus, a smaller species, escaped at approximate 100°. N. sylvestris escaped in the direction almost opposite to the approach of a
looming stimulus from back, front and side (180°; Dupuy et al., 2011). As mentioned above, G. sigillaus had a higher response rate, but G. bimaculatus had a higher accurate escape direction (closer to ±180°; Kanou et al., 2006). N. sylvestris escaped at 169° relative to the direction of the stimulus when an object stimulated from behind, and escaped at 156° when an object stimulated from the side (Figure 1; Dupuy et al., 2011).

**Figure 1. Typical angular coordinate system.** The right turn was reported as a positive angle; the left turn was reported as a negative angle.

*Escape Strategy – Locust*

In regard to the escape response of the locust, *Schistocerca gregaria*, the locust mostly jumped away from a looming stimulus, but in some trials walked away from the stimulus or only cocked its hind leg (Santer et al., 2005).
When locusts were stimulated by a looming object, the response rate was higher than 95% (including jumping, cocking and walking). In terms of the escape direction, its jump was largely forward (±50°; Santer et al., 2005). When the locust jumped away from the stimulus, it used its foreleg to pivot toward the final jump trajectory and then extended its foreleg while its hind leg was releasing to perform a jump behavior. There was no significant difference in regard to left and right escape trajectory. The foreleg motor program was independent of hind leg motor program, since the locust could decide the escape trajectory after its hind leg flexion (Santer et al., 2005).

**Escape Strategy – Fly**

Regarding the escape response of the fruit fly, *Drosophila melanogaster*, the fly mostly jumped and flew away from a looming stimulus, but sometimes flew without first jumping (Card, 2012; Card and Dickinson, 2008).

The escape direction in flies was approximate 180° from the looming stimulus (Card, 2012), including a change of its trajectory by approximate 90° within 100ms during the initial response (Tammero and Dickinson, 2002). *Drosophila* jumped to the opposite side when a looming object came from the back or from the front side, but when a looming object approached from the side, it jumped at the angle between 36° - 72° and
72° - 108° (Figure 1). This forward bias response might be elicited by attractive odors or internal cues, which were always in the forward direction (Card, 2012).

*Escape Strategy – Cockroach (Periplaneta americana)*

In regard to the escape response of the cockroach, the escape response rate of *P. americana* was 100% when its femur or metathoracic leg was stimulated by touch (Comer *et al.*, 1994), 94% - 96% for air-puffs (Stierle *et al.*, 1993) and ~90° for air-puffs (Camhi and Tom, 1978). The initial movement of escape in the cockroach, *P. americana*, was first a pivot turn away from wind or live frogs, with the pivot point located in the posterior region of its body, followed by a walk. The escape response proved a successful strategy, allowing the cockroach to avoid predation in 18/19 instances with live frogs (Camhi and Tom, 1978).

Although cockroaches usually turned away from the stimulus, they did occasionally turn toward to the stimulus (3% - 19% based on Camhi and Tom, 1978, Comer and Dowd, 1987, Domenici *et al*. 2009, Stierle *et al.*, 1993). Furthermore, cockroaches sometimes turned away from the stimulus again after they turned towards to the stimulus, which was called “overshooting” by Domenici (2009). The distribution of turn angles were distributed differently for away and towards responses. Based again on (Camhi and Tom, 1978, Comer and Dowd, 1987, Domenici *et al*. 2009, Stierle *et al.*, 1993), the
range of away responses was much greater (35° - 72°) than the range of toward (15° - 37°) responses.

Sensory Behavior of Escape
The escape response may be mediated by different sensory stimuli (Ye et al., 2003), such as cerci, vision, and antennae; or a combination of sensory modalities.

Cerci: Cerci, which are a pair of appendages at the backside of many insects, contain wind-sensitive filiform hairs that are highly and directionally sensitive to wind. The cerci have been studied mostly in Orthopteras and Dictyoptera, but their morphology, filiform hairs, and central targets varies broadly across insects (McGorry et al., 2014).

Afferent activity is evoked by wind-mediated cercal displacement in all directions (Goldstein and Camhi, 1988). Subsequently, cercal afferents excite giant interneurons in the ganglia of the cockroach. These wind-sensitive interneurons (WSIs), located in the ventral intermediate tract (VIT) and dorsal intermediate tract (DIT), have been implicated in the wind-evoked response (Camhi and Nolen, 1981). Four different species of cockroaches, P. americana, Blattella germanica, Blaberus craniifer and G. portentosa, all possess ascending WSIs in the abdominal connectives, but the
magnitude of their response to wind varies (weakest in *G. portentosa*, strongest in *B. craniifer*, McGorry *et al.*, 2014), paralleling the magnitude of their escape response.

There is evidence that cercal receptors are necessary for the wind-evoked escape response. In the cockroach, *P. americana*, there was no detectable movement evoked by wind stimulation from any angle after the ventral cercal surfaces were covered with adhesive (Camhi and Tom, 1978), effectively ablating the cercal receptors. Further, cerci ablation decreased (from 350 mm s\(^{-1}\) to 238 mm s\(^{-1}\)) escape velocity and escape distance (from 1017 mm to 771 mm; Ye *et al.*, 2003).

Similarly, in the cricket, *G. bimaculatus*, unilateral or bilateral cercal ablation (cerci were cut off at the base) reduced their response to wind dramatically. The response rate dropped from 46.0% to 0% after bilateral cercal ablation, and from 48.1% to 5.5% after unilateral cercal ablation (Kanou *et al.*, 1999). In *G. sigillatus*, the response rate also dropped from 97.2% to 2.7% following cercal ablation (Kanou, 2006). These results show that mechanosensory filiform hairs on the cerci are necessary for the escape response in crickets (Kanou *et al.*, 1999, 2006). However, there is evidence that the cercal receptor might not be absolutely necessary. The escape rate decreased, but the direction of the escape behavior of *G. sigillatus* did not change after the unilateral cercal ablation, suggesting that cercal receptors can change the response rate but not
determine the escape direction. However, the situation was different in *G. bimaculatus*, where both rate and direction were decreased (Kanou *et al.*, 2006)

**Vision:** The visual system varies among insects. In some insects, visual cues may be an important part of their escape strategy, because they (e.g. locust and fly) have been shown to require visual information for escape (Card, 2012; Santer *et al.*, 2005). However, in the cockroach, *P. americana*, there was no change in escape direction when vision was blocked (Ye *et al.*, 2003). Further, wind-evoked response rate in crickets were similar for both light and dark background (Kanou *et al.*, 2014).

In contrast, vision is important to the escape response to looming stimuli in the fly and locust (Card 2012). In *Drosophila*, visual escape is due to a pair of large descending interneurons, the giant fiber (GFs), and also involves additional central neurons (Card, 2012). In the visual system of the locust, the lobula giant movement detector (LGMD, O’Shea and Williams, 1974) and the descending contralateral movement detector (DCMD; Rind, 1984) respond to an approaching object (Judge and Rind, 1997). DCMD responses differed from different azimuthal (angle) directions (Guest and Gray, 2006), and there were at least three descending pathways (including DCMD, DIMD, and LDMCD) that could trigger the locust escape jump (Card, 2012).
Specific Aim

Although escape responses were readily evoked in the cockroach, *P. americana*, it is unclear if it can be evoked in the Madagascar cockroach (*Gromphadorhina portentosa*). Erickson and colleagues (2015) showed that electrical stimulation, of both cerci and antennae, could generate an escape response. However, in other reports (Clark and Triblehorn, 2014; Olsen and Triblehorn, 2014), it was indicated that wind could not elicit the escape response.

The goal of this study was to investigate the escape strategy of the Madagascar cockroach, *G. portentosa*, to looming and heat stimuli. This species has been minimally studied, though currently popular as a pet, and moves slower and is more stationary compared with other cockroach species (e.g. *P. americana*). In this study, cockroaches were stimulated with a looming ball projected toward the cockroach and tarsi were individually stimulated with heat. The escape behaviors were recorded with high-speed video. The hypothesis of this study, based on previous studies of cockroaches and crickets, was the Madagascar cockroach would escape opposite to the looming object and the heat stimulus.
Methods

Insect

Adult Madagascar cockroaches (*Gromphadorhina portentosa*), 51 – 76 mm long, were used. Adults were wingless, slow moving and tended to remain stationary. Cockroaches, purchased from a commercial vendor (New York Worms, Long Island, NY), were fed with carrots, dog food and water gel 3 times every week and kept in a transparent glass tank at 23 – 24 °C (room temperature) and 30 – 70% relative humidity with the ambient environmental light/dark cycle (Haynes, 2005). Experiments were conducted in the same environment during the daytime.

To prepare the cockroaches for the experiment, two small circular spots (the diameter approximately 1.0 mm; e.g. Figure 4) was marked with a white pen (AP ACM, Japan) on the center line of a cockroach without anesthesia, and then the cockroach was restrained by an 8.0 cm (internal diameter) acrylic tube and placed on a circular white primed canvas platform (25.5 cm in diameter; Figure 2). After about 3 minutes, the cover was removed gently. If the cockroach did not move, a trial was conducted.

Looming stimuli

The first series of experiments tested the response of the cockroach to looming stimuli. A ball (2.5” diameter black polystyrene) was the looming stimulus object, which was
projected at 1 m/s toward the cockroach at a 45° vertical angle. The ball never hit the 
cockroach (Figure 2). The ball stopped with its edge close to the edge of the cockroach, 
which still allowed the camera to record the entire cockroach from above vertically. 
When stimulating from the front (directions 0°, +45°, -45°; Figure 3A), care was taken to 
insure the ball would not hit cockroach's antennae.

Heat stimuli
Heat was delivered to the tarsi with a 980nm infrared laser (11 watts, B&W TEK, 
Wilmington, DE) focused by a condenser lens (Figure 2). In the event the cockroach did 
ot respond, stimulus duration was limited to 1 second to prevent damage.

Video Recording
To record video, a high-speed camera (IDT, monochrome`, 650 fps, 25mm lens, f 5.8 
aperture) controlled by IDT software (Motion Studio) and a low heat LED ring were used 
(Figure 2). Each video was 3-second in duration and triggered at the onset of the laser 
or looming stimulus.

Experimental protocol
Each cockroach was stimulated from 8 directions for the looming experiments (Figure 
3A) and 6 locations for the heat experiments (Figure 3B), which were then repeated 3
times for a total of 24 or 18 trials per cockroach. The sequence of 8 or 6 directional locations was randomized for each cockroach.

**Movement Analysis**

After the videos were recorded, ProAnalyst (Xcitex, Cambridge, MA) was used to track the movement of cockroaches based on the two marked spots on the back of the cockroach. The calculated mid-point of the cockroach was used to quantify *translation* (linear movement in the horizontal plane). The angle of the line between the two marked spots was used to determine the turn *angle*. Total angular change was specified as the maximum change in angle. Total translational direction and magnitude were specified as the change from beginning to the end of the movement..

Data were analyzed with custom routines written in Matlab (MathWorks, Inc., Natick, MA) by Corey Cleland. Statistics on movement translational direction and angle were computed with a Watson-Williams “circular ANOVOA” test (Oriana, KCS, Wales, UK). Graphs were created in Sigmaplot (Systat Software Inc., San Jose, CA). Statistical alpha was set at 0.05. Boxplots represent median, 25-75% and 10-90%.
Looming Experiment

Heat Experiment

45 degrees
black 2.5" ball

650 fps camera
LED light
laser
primed canvas

Figure 2. Experiential equipment and Set-up.
The primed canvas circular experiential platform (diameter was 25.5 cm). This platform was used as the experimental field, and a cockroach was demotivated to escape prior to the stimulus by an acrylic tube.
The ball looming system. The looming object, a 2.5" polystyrene ball, was propelled at the cockroach at 45 degrees with an air cylinder driven by 11 psi.
Camera, light and the laser. A high speed video camera (IDT, 650 fps, 25mm lens, f 4 aperture) recorded the movement. The laser (980nm infrared laser (11 watts) was to generate the heat to stimulate the cockroach’s tarsi.
Figure 3. Stimuli direction.
(A) The looming stimuli. The cockroach was stimulated by a looming ball from 8 different directions.
(B) The heat stimuli. Six tarsi of each cockroach were simulated by heat generated by the laser.

Results

Aversive stimuli delivered to Madagascar cockroaches (n=17) evoked escape responses in 27.4% of 252 trials (11.4% heat, 50.5% looming). Figure 4 shows a typical escape response to a heat stimulus delivered to the back-left tarsus for video (A) and tracked locations (B). The cockroach both turned and translated in the direction
opposite to the stimulated tarsi (Figure 4). In the looming experiments, the cockroach also responded to the stimulus (Figure 5). However, the turn was typically small and often in the opposite direction. Further, the escape translation distance was shorter compared with the heat stimulation.

**Figure 4.** A typical escape trajectory of a Madagascar cockroach stimulated by heat. (A) 3 frames (1000 ms) of escape trajectory. (B) The stick diagram of the same escape trajectory as A. The filled circles correspond to the two tracked white marks on the cockroach. The arrows correspond to the stimulus location (back-left tarsus).
Figure 5. A typical escape trajectory of a Madagascar cockroach stimulated by a looming object. (A) 3 frames (50 ms) of escape trajectory. (B) The stick diagram of the same escape trajectory as A. The blue dots correspond to the two tracked white marks on the cockroach. The arrows correspond to the looming direction (back-left tarsus).

Overall, although escape translation of the cockroaches was directed away from both heat and looming stimuli, the total distance traveled (translation) was greater for heat than for looming stimuli (Figure 6A).
Figure 6. Frequency histograms of total movement. Frequency histograms of total translation for looming (left) and heat (right) evoked responses.

In the looming experiments (Figure 7), cockroaches turned (51/103, 49.5%) and translated (72/103, 69.9%) away from the stimulus. In contrast, for heat stimuli (Figure 8), cockroaches more reliably turned (132/149, 88.6%) and translated (145/149, 97.3%) away from the stimulus.
Figure 7 The escape trajectory stimulated by a looming object. (A) The escape direction of Madagascar cockroaches stimulated by a looming object (51 away, 52 towards, N = 103). (B) The escape translation of Madagascar cockroaches stimulated by a looming object (72 away, 31 towards, N = 103).
Figure 8. The escape trajectory stimulated by heat. (A) The escape direction of Madagascar cockroaches stimulated by heat (132 away, 17 towards, N = 149). (B) The escape translation of Madagascar cockroaches stimulated by heat (145 away, 4 towards, N = 149).

The dependence of turning angle on stimulus location or direction was different for stimulation by looming or heat stimulation (Figure 9). For looming, the turning angle was always close to 0° and did not depend on stimulus angle (Figure 9A; p = 0.1, Williams-Watson). For heat, the translation direction varied between ±50° and depended significantly on stimulus location (Figure 9B; p = 0.0001, Williams-Watson).
Figure 9. The turning angle of a Madagascar cockroach. (A) The turning angle for looming stimuli direction. The angle of turn did not depend on looming direction ($p = 0.1$; $n = 21/angle$, Williams-Watson). (B) The turning angle for heat stimuli location. The turn angle depended significantly ($p = 0.0001$, $n = 30/angle$, $r^2 = 0.416$, Williams-Watson) on heat location. The numbers correspond to tarsi (Figure 3B).

Since Madagascar cockroaches are symmetric, it was considered as the same stimuli in the looming experiment when a Madagascar cockroach was simulated by a looming object from the direction $45^\circ$, $90^\circ$, $135^\circ$ and the direction $-45^\circ$, $-90^\circ$, $-135^\circ$, respectively (Figure 3A); it was also considered as the same stimuli in the heat experiment when its tarsus was simulated from the direction $1$, $2$, $3$ and the direction $6$, $5$, $4$, respectively (Figure 3B). Consequently, stimuli and response from right-sided stimuli were reflected to the left-sided to combine results.
In the reflected analysis (Figure 10), similar results were obtained. There was no significant dependence of turn angle when cockroaches were stimulated by a looming object ($p = 0.07$, Williams-Watson). In contrast, for heat stimuli, the angle of turn depended significantly on stimulus location ($p < 0.0003$, Williams-Watson). Thus, heat-evoked turns depended not only on which side the stimulus was given, but also on the degree of laterality of the stimulus.

**Figure 10. The reflected turning angle of a Madagascar cockroach.** (A) The turning angle of a Madagascar cockroach did not depend on the reflected looming stimuli direction ($p = 0.07$, $N = 103$). (B) The turning angle of a Madagascar cockroach depended on the reflected heat stimuli location ($p < 0.003$, $N = 149$, $r^2 = 0.09$).
The dependence of translation on stimulus location or direction was also different for stimulation by looming or heat stimulation (Figure 11). For looming, the translation direction ranged from \(-180^\circ\) to \(+180^\circ\) and depended on stimulus angle (Figure 11A; p < 0.0001). For heat, the translation direction varied similarly and also depended on stimulus location (Figure 11B; p < 0.0001, Williams-Watson). Since the slopes were \(-35^\circ\) and \(54^\circ\) per stimulus “step” (8 for looming = \(280^\circ\), 6 steps for heat = \(324^\circ\)), the resulting direction of translation was close to directly away from the stimulus.

**Figure 11. The escape translation direction of a Madagascar cockroach.** (A) The escape translation direction for looming stimuli direction. The translation direction depended on looming direction (p < 0.0001, slope = \(35.6^\circ/\text{angle}\), N = 103, \(r^2 = 0.487\)). (B) The escape translation direction for heat stimuli location. Responses direction depended significantly (p < 0.0001, slope = \(54.2^\circ/\text{angle}\), N = 149, \(r^2 = 0.906\)) on heat stimulus location.
In the reflected analysis (Figure 12), translation direction for both looming (p<0.001, Williams-Watson) and heat (p<0.001, Williams-Watson) varied significantly with stimulus direction or location, demonstrating that the response depended on stimulus laterality (ipsilateral angle ranging from front to back).

**Figure 12.** The reflected escape translation direction of a Madagascar cockroach. (A) The escape translation direction depended on the reflected looming stimuli direction (p < 0.001, n = 62.2/angle, N = 103, $r^2 = 0.46$). (B) The escape translation direction of a Madagascar cockroach depended on the reflected heat stimuli location (p < 0.001, n = 58.1/angle, N = 149, $r^2 = 0.72$).
Discussion

Summary
In contrast to a published report (Olsen and Triblehorn, 2014), the escape response of the Madagascar cockroach can be readily elicited by heat and looming stimuli, although the magnitude of the response to the looming stimulus used in these experiments was small compared to crickets (Camhi and Tauber, 1995) and cockroaches (Camhi and Tom, 1978). The escape response consisted of both a turn and translation with heat but only a translation with looming. Importantly, reflected analysis showed that the cockroaches response varied with both laterality (which side the animal stimulated) and degree of laterality (where on the side the animal was stimulated).

Comparison to Pervious Studies
Two reports suggested that there is neither a wind-evoked running escape response (Clark and Triblehorn, 2014) nor a terrestrial response or flight (Olsen and Triblehorn, 2014) in the Madagascar cockroach. Further, Erickson and colleagues were only able to evoke consistent escape responses with combined artificial (electrical) stimulation of both cerci and antennae. However, these results showed that this species responded to both heat and, to a lesser extent, looming. The explanation for the differences may be two-fold. First, responses, especially to looming, were small and may have been
missed. Second, heat, which produced the strongest responses, has not been previously used.

**Sensory Mechanisms**

Cercal activation of WSIs, located in the VIT, is to initiate the turning movement (Camhi and Nolen, 1981; Ye et al., 2003). However, in *G. portentosa* the WSI provides weaker input to the premotor/motor neuron than in other cockroach species shown by lower spike counts (*P. americana*; McGorry *et al*., 2014). Therefore, the cerci in *G. portentosa* may have less sensitivity or central strength when stimulated by wind.

However, there might also be possible that another sensory evoked the escape response in *G. portentosa* for the looming experiments, because *G. portentosa* might use the visual information to evoke the escape response when an object was approaching. Regarding the escape response to heat, while clearly there must be heat sensors in the tarsi, there are apparently no previous studies in the literature.

**Conclusions**

These results demonstrate that Madagascar cockroaches, like other insects and in contrast to the existing literature, execute an escape behavior in response to aversive stimuli. Surprisingly, however, heating of their tarsi evoke far stronger responses than
looming stimuli that mimic predators. These results raise questions about the normal
degree of threat faced by Madagascar cockroaches from looming predators and
terrestrial sources of heat.
References


