

Individual Thigmotactic Preference Affects the Fleeing Behavior of the American Cockroach (Blattodea: Blattidae)

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Abstract

Positive thigmotactic behavior is associated with the ability to hide from predators and is important to explain aggregation and collective patterns in various animals. For example, this behavior has been observed in woodlice, domiciliary cockroaches, ants, and fish. Lately, research on different species is focused on the importance of animal personality for ecological and evolutionary processes, individual fitness and group cohesion. In fact, it is generally expected to find some degree of interindividual consistent differences for a behavior, unless specific circumstances, like predator attacks, hide the presence of personalities. In this research, we analyzed the individual thigmotactic preference of domiciliary cockroaches (*Periplaneta americana* (Linnaeus, 1758) (Blattodea: Blattidae)) and how it affected the fleeing behavior of isolated individuals inside a shelter after receiving a light stimulus. We notably highlight how isolated individuals show different consistent preferences regarding their position in the shelter, which is due to the individual thigmotaxis level, before the fleeing behavior. During the fleeing itself, cockroaches nearer to the wall, and therefore with more positive thigmotaxis, showed slower reaction latencies to the stimulus. We propose that thigmotaxis homogenizes the interindividual differences among individuals and is important to explain the individual and collective fleeing behavior.

Key words: thigmotaxis, disturbance, fleeing behavior, animal personality, domiciliary cockroach

Landscape heterogeneities can affect the spatial distribution of organisms by influencing their movement patterns. For instance, habitat edges or patch boundaries can help the aggregation or modify the movement patterns of animals with positive thigmotaxis (Jeanson et al. 2003). Positive thigmotactic behavior, or the tendency to remain close to walls or edges, is widespread in different taxa (Grossen and Kelley 1972, Kallai et al. 2007, Sharma et al. 2009) and can be modulated by several factors. For example, positive thigmotaxis decreases in a familiar environment and during exploration, and increases under stressful situations (Durier and Rivault 2003, Sharma et al. 2009). In addition, positive thigmotactic behavior is a crucial factor to explain and understand the aggregation and movement of several species such as woodlice, domiciliary cockroaches, ants, or fish (Dussutour et al. 2005, Bell et al. 2007, Devigne et al. 2011, Boulay et al. 2013, Webster and Laland 2015) and can be used as a proxy for behavioral traits such as boldness or shelter use (Carlson and Langkilde 2013, Webster and Laland 2015). One possible reason why thigmotaxis has been selected for so many species is that it accelerates a search process in certain conditions, and thus

is a kinetically efficient behavior, as has been shown by theoretical research (Calandre et al. 2014).

Recently, several authors have studied thigmotaxis in the context of individual behavioral differences (Carlson and Langkilde 2013, Webster and Laland 2015). Behavioral variability and plasticity have evolved, and are maintained, through numerous processes that ultimately allow animal populations to adapt to different environmental conditions (Dall et al. 2004, Sih et al. 2004, Carrete and Tella 2010, Dingemanse et al. 2010, Smith and Blumstein 2010, Adriaenssens and Johnsson 2013). In this study, we define personality as the presence of behavioral differences between individuals that are consistent over time for a specific behavior (Dall et al. 2004, Bell et al. 2009, Dingemanse and Wolf 2010, Réale et al. 2010, Webster and Ward 2011, Adriaenssens and Johnsson 2013, Planas-Sitjà et al. 2015). The presence of these personalities is widespread and raises the complexity of group dynamics. For example, the fission–fusion dynamics of groups of bats (Kerth 2010) and birds (Aplin et al. 2013) is influenced by the personality of each individual; the aggregation dynamics of *Periplaneta americana* (Linnaeus,

1758) (Blattodea: Blattidae) is influenced by individual and group personalities (Planas-Sitjà et al. 2015); and individual personality in stickleback fish strongly affected the group's structure, movement dynamics, and foraging behavior (Jolles et al. 2017). Regarding fleeing behavior, different studies have found the existence of behavioral syndromes (Carter et al. 2010, Niemelä et al. 2012, Seltmann et al. 2012, Cooper Jr and Blumstein 2015) and that some events, like an increase of risk or stress, might break apart individual personalities (Niemelä et al. 2012, Cote et al. 2013, Wright et al. 2017).

It is in this context, using a gregarious species, that we performed the current study aiming to analyze the presence, or absence, of personality in the context of thigmotactic behavior, and its effects during fleeing, of an isolated individual. Our biological model was the negatively phototactic American cockroach (*P. americana*), which forms aggregations in dark, warm, and damp places during daylight hours (Bell and Adiyodi 1982, Canonge et al. 2011). *P. americana*, when suddenly illuminated in their resting place, initiate a fleeing response (Okada and Toh 1998, Domenici et al. 2008). Domiciliary cockroaches have a very strong tendency to follow a wall, even while fleeing (Camhi and Johnson 1999, Durier and Rivault 2003). Consequently, knowing that domiciliary cockroaches express different personalities during their sheltering process (Planas-Sitjà et al. 2015), we used their light avoidance behavior to investigate the relationship between thigmotaxis and the possible behavioral consistency before and while fleeing.

Materials and Methods

Rearing Conditions

The cockroaches were taken from the rearing room of the Université libre de Bruxelles (ULB). *P. americana* has been reared in the ULB since 2002 in five Plexiglas vivaria (80 × 40 cm and 100 cm high) in which cardboard tubes are hung from the walls to serve as shelters. Groups of around 20 individuals were weekly exchanged between vivaria. Each vivarium had around 1,000 individuals, comprising males, females, and larvae from all developmental stages. They were provided with dog pellets and water ad libitum. The rearing room was kept at 26 ± 1°C with a photoperiod of 12:12 (L:D) h.

Experimental Set-Up

Our study was carried out using the experimental protocol described in detail in the study by Laurent Salazar et al. (2013). The experiments were performed in a circular arena (Fig. 1) that had an electric fence to prevent the cockroaches from escaping (Laurent Salazar

et al. 2013). The floor of the arena was covered with white paper (120 g/m²), which was changed after each experiment to prevent any chemical marking.

A plastic ring (interior diameter: 25 cm, height: 4.5 cm, width: 5mm), central within the arena, constituted the shelter. Two openings of 3 × 1.5 cm placed symmetrically opposite to each other were the only ways out of the shelter. A glass cover was placed on top of the ring to allow the observation of the interior.

A light bulb (Philips [Amsterdam, The Netherlands] A55 FR, 100 W) centered on the arena at a height of 50 cm above the glass was switched on at the beginning of each experiment. When the light was turned on, only the inside of the shelter received ~1,700 lx. (luxmeter Testo 545, Testo NV/SA [Lenzkirch, Germany], resolution: 1 lx). The rest of the arena, and of the room, was only illuminated by red light (0 lx). This arrangement allowed us both to see and to keep the room 'dark' for the cockroaches (Mote and Goldsmith 1970).

Experimental Procedure

Only adult males (without external damages such as wing damage or missing leg segments) were tested to exclude any behavioral variations related to the ovarian cycle (Paterson and Weaver 1997). Isolated individuals (24 replicates) were randomly taken from the rearing room and placed the day before the trial in plastic containers (36 × 24 and 14 cm in height). They were kept in the dark until the beginning of their respective trials. Each cockroach was tested three times in total, with a 2-d interval between tests. The cockroaches had access to dog pellets (Tom & Co., Delhaize Group, Brussels, Belgium) and to a piece of cotton soaked in water.

Before the start of each trial, the arena was cleaned with denatured ethanol, and a new sheet of paper was placed on the floor. After 10 min, the individual was introduced under light CO₂ narcosis into the shelter (the openings were closed), as is standard procedure (Jeanson et al. 2003, 2005; Halloy et al. 2007), and remained there for 30 min. After this waiting period, the openings were opened, and the light was turned on. A webcam was used to record the cockroach's behavior inside the shelter (20 frames/s) and recorded the individual's response for 5 min or until the cockroach had left the shelter. As noted above, during the night, *P. americana* are active and leave their shelter to forage (Bell and Adiyodi 1982). For this reason, all trials were performed during daylight hours corresponding to the resting phase of *P. americana*.

Analysis

From the video recordings, we analyzed the following parameters:

- (1) The position (radius from the center of the shelter), orientation, and contact with the wall of each individual prior to the turning on of the light (t_0). To analyze the orientation of the individuals, we calculated the angle between the head–abdomen axis of the cockroach and the axis going from the shelter wall to the center of the arena and passing through the middle of the cockroach. If the angle was comprised between +45° and -45°, we considered that the individual was facing toward the shelter wall (Supp material [online only]).
- (2) The reaction time (RT) for each individual was the time interval between the turning on of the light (t_0) and the initiation of its fleeing behavior. We considered an individual to be reacting when it rotated its body or moved forward/backward. When an individual was walking prior to t_0 (0.32 of all trials), it was removed from the analyses. We consider that the immobile/mobile states are different because mobile individuals (already

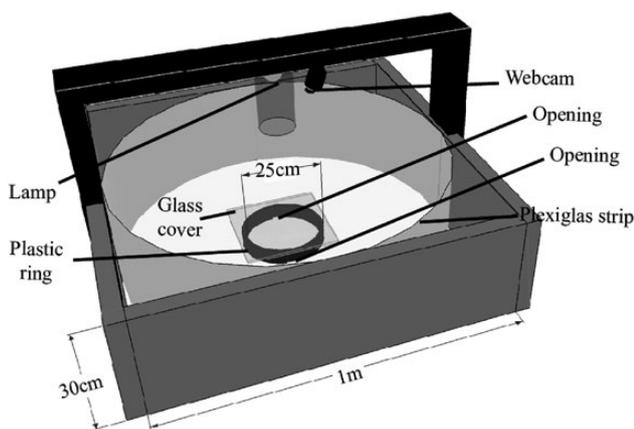


Fig. 1. Experimental set-up. Individual cockroaches were placed inside the plastic ring.

walking) were more prompt to flee than the immobile ones when light was turned on.

We used survival curves (or decay curves) to analyze the distribution of these parameters. Although the name includes the term 'survival', it can be used to analyze any kind of experiment where the results are expressed as a time to an end point. For the comparison of survival curves, we used a log-rank test (Motulsky 1999). For the analysis of curve fittings and linear regressions, we used Kolmogorov–Smirnov test and *F*-test, respectively.

To compare distributions, we used chi-square test when the conditions allowed it, otherwise we used two-sample Kolmogorov–Smirnov tests. Since our values did not meet the conditions for parametric tests, we used Kruskal–Wallis and Mann–Whitney tests to compare differences between days and individuals, depending if more than one comparison was being carried out or if the values were paired.

We used the Kendall's coefficient of concordance (*W*) for concordance assessment (Kendall 1938; Kendall and Smith 1939). Kendall's coefficient of concordance (*W*) compares the stability of rank positions for each group during the trials. The values of *W* range from 0 (no concordance of ranks) to 1 (complete concordance). We compared the observed *W* coefficients with the 'Kendall random distribution' (KRD) as explained by Planas-Sitjà et al. (2015). The KRD is the theoretical distribution of the *W* coefficients for random rank orders of the same number of experimental groups and repetitions (e.g., 24 groups and 3 repetitions and *N* = 1,000). We performed a *Z*-test to test the significance of the difference between the observed *W* coefficients and the corresponding KRD (Zar 2010, Laurent Salazar et al. 2015, Planas-Sitjà et al. 2015). In this case, we assigned the value of 0 s to the RT of immobile individuals. This was necessary to be able to quantify personality traits and allowed us to consider the idea of individuals being more prompt to react (with an RT value of 0) when analyzing their reaction personality (e.g., see whether an individual was always ready to flee, already moving or slow to react).

To analyze the influence of the contact with the wall on cockroach orientation, we used a one-tail binomial test to compare their observed orientation and a theoretical random expectation of facing toward the wall (*P* = 0.25).

Results

Before the Disturbance

The distribution of the position of the individuals within the shelter, the number of moving individuals, and the number facing toward

the wall of the shelter prior to t_0 did not significantly differ between days (Table 1). When we compared the number of times each individual was moving, and the number of times it was facing toward the shelter wall, against a theoretical random distribution, we found no significant difference (Table 2). However, our results showed that individuals significantly differed from each other and presented distinct preferences regarding their position respective to the center of the shelter (Figs 2a and 3; Table 2).

This personality regarding their position has interesting consequences for their thigmotactic preferences. Since individuals touching the wall did so with their antennae, it was their length that limited the distance where touching was possible. Indeed, the probability of touching the wall follows a logistic function and shows that individuals placed more than 4.6 cm from the wall (7.9 cm from the center) never touch the wall, while those closer than 4.6 cm do

$$\text{Touch} = \frac{1}{1 + e^{10.7(-\text{radius})}}, \quad R^2 = 0.8,$$

two-sample Kolmogorov–Smirnov test: *D* = 0.18, *P* = 0.17; Fig. 4). The high steepness of the fitting (coefficient value = 10.7) clearly shows how touching or not touching the wall is close to an all-or-none response. In other words, all individuals within reach of the wall, will touch it. This allowed us to divide the individuals into two groups regarding their thigmotactic preference: high thigmotactic level (<4.6 cm from the wall) and low thigmotactic level individuals, HTL and LTL, respectively. Across 3 d, we observed 28 LTL individuals and 44 HTL individuals.

In addition, we analyzed the influence of the thigmotactic level on cockroach orientation. In the case of the LTL individuals (*N* = 5/28 were facing toward the wall), there was no significant difference between our observations and theoretical random expectation of 0.25 (one-tailed binomial test: *P* = 0.26). However, the HTL individuals (*N* = 17/44) had a significant tendency of orienting themselves toward the shelter wall (Binomial test: *P* = 0.032).

During the Disturbance

The relationship between the thigmotactic level and RT among the immobile individuals (22 distinct individuals were immobile; during the 3 d, we observed 49 immobile individuals) was clear. Indeed, immobile HTL individuals (31 individuals) differed in their RT from the LTL (18 individuals) ones (Mann–Whitney test (mean ± SD): RT HTL (27.4 s ± 38) and RT LTL (7 s ± 8.2): *U* = 165, *P* = 0.024).

These results indicate clearly that the thigmotactic level of individuals during rest has an influence on their fleeing behavior: HTL

Table 1. Results of the interday behavioral comparison

	Day I	Day II	Day III	Comparison between days
Spatial distribution	Homogenous Chi-square: $X_3^2 = 1.69$, <i>P</i> = 0.64	Homogenous Chi-square: $X_3^2 = 4.91$, <i>P</i> = 0.18	Homogenous Chi-square: $X_3^2 = 0.29$, <i>P</i> = 0.96	No difference Chi-square: $X_6^2 = 8.2$, <i>P</i> = 0.22
Individuals facing toward the shelter wall	7	8	7	No difference Chi-square: $X_2^2 = 0.13$, <i>P</i> = 0.94
Number of moving individuals	8	6	9	No difference Chi-square: $X_2^2 = 0.89$, <i>P</i> = 0.64
RT: $\lambda = 1/RT$ $\lambda = 0.08 \pm 0.02$ per s	Exponential distribution $R^2 = 0.83$; Kolmogorov–Smirnov test: <i>D</i> = 0.18, <i>P</i> > 0.90	Exponential distribution $R^2 = 0.96$; Kolmogorov–Smirnov test: <i>D</i> = 0.11, <i>P</i> > 0.99	Exponential distribution $R^2 = 0.92$; Kolmogorov–Smirnov test: <i>D</i> = 0.13, <i>P</i> > 0.99	No difference $X_2^2 = 1$, log-rank test: <i>P</i> = 0.60

The table shows the daily result for each measure and their comparison between days.

Table 2. Summary of the interindividual differences

	Presence of interindividual difference?	Consistent interindividual difference?
Spatial distribution	Yes Kruskal–Wallis test: $H_{23} = 41.98, P = 0.009$	Yes Kendall's $W = 0.58, Z = 3.15, P = 0.0016$
Individuals facing toward the shelter wall	No chi-square: $X_1^2 = 2.6, P = 0.27$	
Number of moving individuals	No chi-square: $X_2^2 = 1.83, P = 0.61$	
RT	No Kruskal–Wallis test: $H_{19} = 20.97, P = 0.34$	No Kendall's $W = 0.39, Z = 0.7, P = 0.48$

The table shows the presence of interindividual difference and its consistency for each measure. Only the spatial distribution of individuals showed interindividual difference, which was consistent across days.

individuals were four times slower to react than LTL individuals (Fig. 3). Nevertheless, we found no consistency in RT within individuals: individuals' RT rankings varied each day (Fig. 2b; Table 2).

Discussion

It is well known that numerous species, including domiciliary cockroaches like the American cockroach, show positive thigmotaxis, and that this thigmotaxis affects the exploration of the environment as well as the individual and collective behavior (Camhi and Johnson 1999, Jeanson et al. 2003, Okada and Toh 2006, Kallai et al. 2007, Baba et al. 2010). In this study, we show that prior to a light disturbance, individuals of *P. americana* displayed clear personalities regarding their thigmotactic preference (being in range to touch the wall, <4.6 cm from the wall, or not) and thus demonstrating that thigmotaxis is a quantifiable personality trait in *P. americana*.

In addition to this, we observed that high thigmotactic level individuals tended to orient themselves toward the wall. It is possible that inside a shelter an individual cockroach will orient itself automatically toward a wall when near to it. However, we are inclined toward the hypothesis that this orientation increases their thigmotactic level when in their resting phase. Indeed, in experiments where cockroaches explore a bigger arena, they position themselves parallel to the arena wall, even when touching it (M-O Laurent, Isaac Planas-Sitjà, personal observation). This is different from our current observations. It is possible that the wall has a different influence on a cockroach's behavior depending on the context. Certainly, in an open and novel space, stressed individuals will tend to be parallel to a wall, move slower, and follow it for protection (Durier and Rivault 2003, Sharma et al. 2009). However, inside a shelter, individuals are arguably less stressed and do not need to position themselves parallel and against the wall.

We clearly show how, for immobile individuals, being in contact with the wall (i.e., high individual thigmotactic preference) had an impact on their RTs, with individuals touching the wall being significantly slower to react. It is possible that such individual differences regarding their position could be the result of different survival strategies. An individual near a wall that reacts slower would be safer by being more cryptic, and running along the wall later to find shelter if needed (Durier and Rivault 2003, Sharma et al. 2009), while an individual further away from the wall would flee faster and find shelter. These different strategies would be advantageous depending on

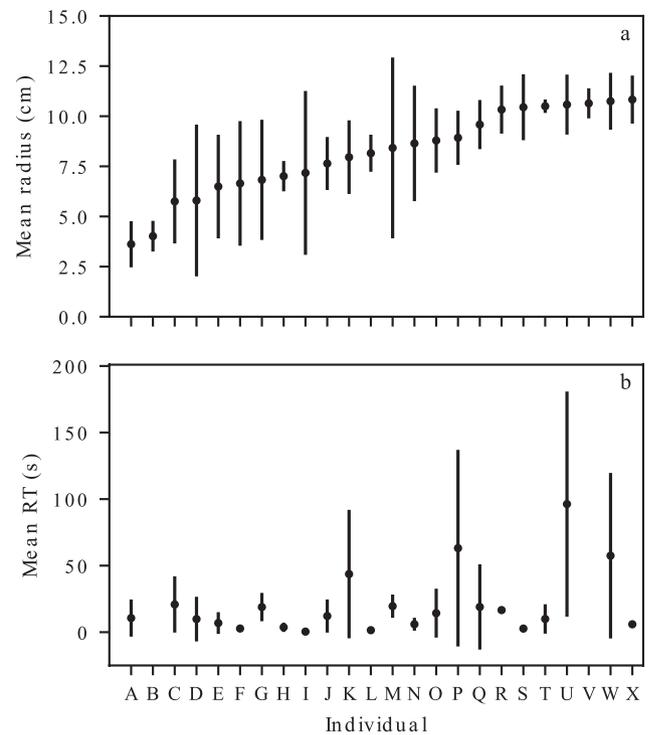


Fig. 2. (a) Average radius (+SD) (the distance from the center of the shelter to the cockroach's body, 0 = center of the shelter). (b) Average RT (+SD) of each immobile individual.

the menace (e.g., kind of predator) or foraging strategy (Hendrie et al. 1998).

The RTs across days were not consistent between individuals, in contradiction with previous studies (McDermott et al. 2014; Stanley et al. 2017) showing consistency in the reaction to a disturbance. It is possible that individuals had different reaction threshold to light disturbances, but the magnitude of the disturbance in our study was such that it overshadowed these differences. Further experiments with different light intensities could provide insights on this

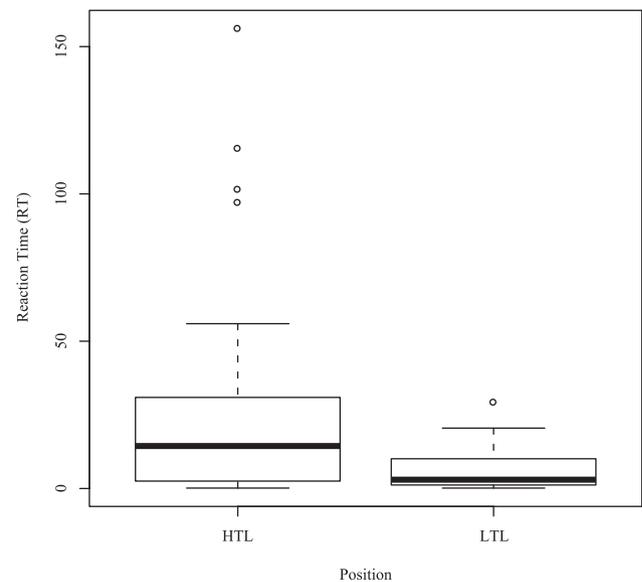


Fig. 3. Boxplot comparing the RT to a light stimulus between HTL and LTL individuals.

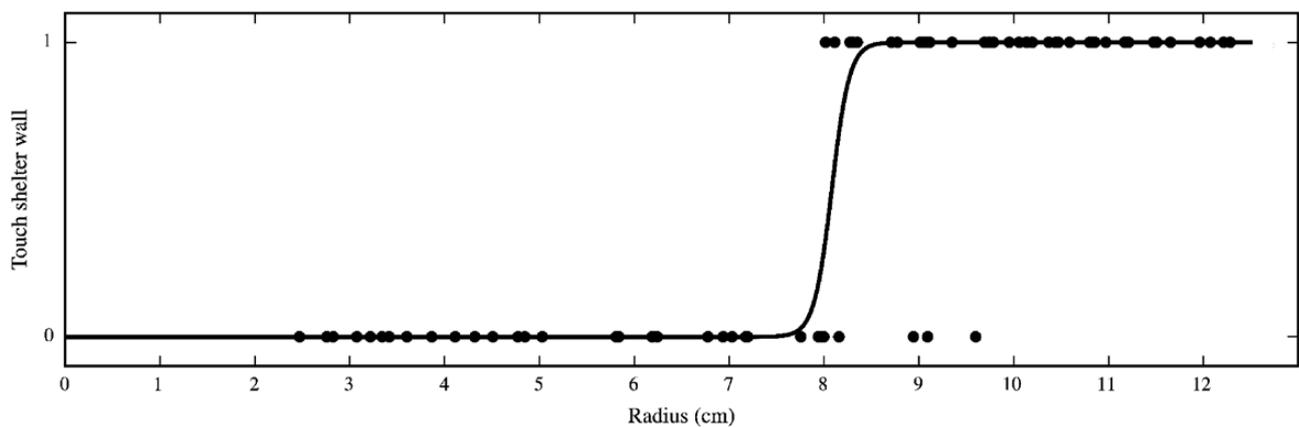


Fig. 4. Contact with the wall of the shelter before the disturbance as a function of the position of each individual (1 = touching, 0 = not touching the wall). The position of each individual is represented as the distance from the center of the shelter to the cockroach's body (i.e., radius).

hypothesis. In addition, the lack of consistency in our study could be due to the thigmotactic behavior, which was missing in the mentioned previous works. We have already seen that thigmotaxis can be influenced by the environment, for example, in domiciliary cockroaches the presence of a wall modifies their exploratory behavior, reducing their speed and increasing their number of stops (Durier and Rivault 2003). Furthermore, it has been shown that being in novel environments increases the tendency of being positively thigmotactic (Simon et al. 1994, Durier and Rivault 2003, Sharma et al. 2009). Considering these results, we hypothesize that the lack of consistency regarding the RT can be explained by the fact that thigmotaxis reduces and homogenizes the interindividual differences between individuals. Indeed, if individuals slow their exploration near walls, and novel environments increase their preference to be near a wall, then it is possible that in our experiments (new environment) individuals increased their tendency to be close to the wall. Thus, individuals that would otherwise display different fleeing thresholds will be positioned close to the wall and show slower RTs when the light is turned on, homogenizing the RT. Experiments with a higher framing rate (higher than 20 fps) could shed some light on this matter, being precise enough to detect interindividual differences in RTs despite the homogenization caused by the thigmotactic behavior.

Regarding the global positioning, we observed that the distribution within the shelter prior to the disturbance was homogeneous. In a prior study, Laurent Salazar et al. (2013, Supp Material [online only]) showed that isolated and pairs of individuals were also homogeneously positioned within a shelter, however individuals in larger groups had a distribution significantly different from a theoretical homogeneous distribution, with an increase in the number of individuals close to the shelter wall compared with the theoretical distribution. This observation, albeit in need of further research, already gives us a glimpse of the difficulties in studying individual preferences in a collective context. By being numerous, due to the gregarious behavior, it is possible that their individual preferences for the wall were amplified (Dussutour et al. 2005), leading to the heterogeneous distribution in favor to being closer to the wall.

Previous studies on fleeing responses have been able to concentrate on the consistency of many behavioral and kinematic traits (e.g., in vertebrates (Marras et al. 2011; Hitchcock et al. 2015) and invertebrates (Stanley et al. 2017)). However, to our knowledge, there is an absence of works concerned about personality traits during fleeing and kinematic traits in insects. In our present study, we

were able to quantify different traits for individuals without the collective context having a potential impact. The quantification of personality on individual thigmotaxis level shed some light on the proximal mechanisms that affect the presence of both individual and collective personality shown in previous studies on collective dynamics under different conditions in *P. americana* (Laurent Salazar et al. 2015, Planas-Sitjà et al. 2015). As positive thigmotaxis has been shown to have evolved in many species and to be important for their behavior and survival (Grossen and Kelley 1972, Kallai et al. 2007, Sharma et al. 2009), we believe that the existence of individual thigmotactic preferences could be extensible to many of these species. How these preferences are maintained within a group and how they affect the collective behavior are key questions for the understanding of the behavioral ecology of gregarious species. The presence of personalities within a group has been seen to have an important impact on the performance of the group during collective behaviors (Brown and Irving 2014, Cronin 2015). There is no doubt that such individual variability also influences collective fleeing behavior. Further studies on gregarious insects and their individual preferences are indeed needed to acquire a complete view of their collective behavior and elucidate how these personalities could be an evolutionary benefit for the collective fleeing response to disturbances. For instance, studies on the positional preferences would allow us to create nonrandom groups consisting of individuals with personality regarding their positioning and their responses to the stimulus. In such a way, it would be interesting to not only link these personality traits with collective fleeing dynamics but also to other behaviors in different situations, such as collective shelter choice, aggregate stability, or food search. Indeed, studies testing such groups could help elucidate the influence of group composition in collective dynamics, especially in research aiming at understanding the link between individual preferences, individual preference amplification, and collective behavior.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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