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Self-amplification as a source of interindividual variability: Shelter selection in cockroaches

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ABSTRACT

Although group effect and collective decisions have been described in many insect species, the behavioral mechanisms involved in the process remain poorly documented at the individual level. We examined how individual behavior depends on the environmental context and we precisely characterized the behavioral rules leading to settlement of individual cockroaches in resting site. We focused on the spatial and temporal distribution of individuals in absence of conspecifics. Using isolated adult males of the cockroach *Periplaneta americana*, we showed that the quality of resting sites and the duration of the settlement exerted an influence on the individual decision-making: the probability of leaving a resting site decreased with the time spent under a shelter. A numerical model derived from experimental data suggested that this simple rule of self-amplification can also account for the interindividual variability.

1. Introduction

In group-living organisms, considerable attention has been turned to the costs and benefits of sociality (Hamilton, 1971; Krause and Ruxton, 2002; Estevez et al., 2007) as well as on the social interactions leading to the formation of various adaptive collective patterns such as foraging trails or nest structures (Hölldobler and Wilson, 1990; Camazine et al., 2001; Conradt and Roper, 2005; Detrain and Deneubourg, in press; Conradt and List, 2009). Such a focus on social issues has caused workers to overlook the importance of the individual behaviors. Even though, a good knowledge of individual behavior is necessary to fully understand the emergence of collective behaviors at the group level, a precise characterization and quantification on how individuals behave in response to environmental heterogeneities are often lacking. In addition, individuals may exhibit an important behavioral variability which is known to exert a major impact on group behavior (e.g. Dussutour et al., 2008). Nevertheless, studies on collective behavior have often considered the group as homogeneous with all group-members being identical (i.e. as equal subunit) and behaving similarly (Camazine et al., 2001; Breckling et al., 2006; Detrain and Deneubourg, 2006). In the wild, a large number of factors such as external (e.g. environmental properties, presence of conspecifics: see Depickère et al., 2008) and internal stimuli (physiology, circadian rhythms, age and learning) modulate the response of individuals. The environment is an important factor regulating the spatial distribution of individuals of a species: settlement or exploration depends on abiotic parameters such as humidity, temperature and light intensity for example. Consequently, for a better understanding of social organization, it is required to study how individuals interact with each other but also how each individual behaves and makes choice in its environment, independently of any social influence.

In this study, we examined the individual choice of a shelter in an urban gregarious cockroach, *Periplaneta americana* (Cornwell, 1968; Leoncini and Rivault, 2005; Saïd et al., 2005), which has been widely used in the field of neurobiology (Huber et al., 1990; Comer and Robertson, 2001; Kwon et al., 2004; Pintér et al., 2005; Clarac and Pearlstein, 2007). This cockroach genus has a worldwide distribution and lives in urban areas (Bell and Adiyodi, 1982; Schal et al., 1984), with potential consequences on human health such as asthma and vector of disease (Rivault et al., 1993; Pai et al., 2003, Salehzadeh et al., 2007). These cockroaches exhibit social interactions but, unlike eusocial insects, they do not show task specialization (Bell and Adiyodi, 1982). During their diurnal resting period, they form mixed clusters of males and females with all instar-nymphs resting in dark and confined places such as cracks and crevices (Bell and Adiyodi, 1982; Grandcolas, 1998; Rivault, 1989; Rivault and Cloarec, 1991). Therefore, the individual decision to settle under a shelter is affected by both the presence of conspecifics (Bell and Adiyodi, 1982; Sempo et al., 2006; Halloy et al., 2007) and its response to the physical characteristics of

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shelters. Here, we examined shelter selection of one individual in response to the heterogeneities of the environment, without any social interaction. Male cockroaches were tested alone in presence of two different shelters (one light and one dark). In such conditions, the decision to settle under a specific shelter arose from the dynamics of transitions between resting in shelters and exploring the arena. The following issues were addressed in this context. How did the physical characteristics of a shelter influence the individual decision to settle? How did the duration of settlement affect the individual probability of leaving the shelter? Did every individual follow the same behavioral rule, or, in contrast, was there any variability in individual responses? More precisely, we analyzed the individual dynamics (i.e. the spatial and temporal distribution) and characterized the behavioral rules leading to cockroach settlement depending on shelter quality. Next, we investigated whether differences between individuals exist in the settlement behavior. Finally, we developed a numerical model based on parameters resulting from our experiments to examine the origin of interindividual variability.

2. Methods

2.1. Studied species

Experiments were carried out on isolated adult males (average length: 4 cm) of the cockroach species *P. americana* (L.) (Dictyoptera: Blattidae). This specie is native to the tropics and currently has a worldwide distribution (see review Bell and Adiyodi, 1982; Schal et al., 1984). *P. americana* is closely associated with human dwellings, food processing industries, and shows dense populations in urban areas. In the wild, these cockroaches aggregate in dark places during the photophase (Bell and Adiyodi, 1982). In the laboratory, cockroaches were reared in an air-conditioned room at 25 ± 1 °C under a 12 h:12 h light:dark cycle. In breeding boxes (length: 80 cm, width: 40 cm, height: 100 cm), all stages of development (ootheca, nymphs and adults) and both sexes were mixed. The cockroaches had access to water and dog food pellets (Tom & Co®) *ad libitum*.

Before each trial, adult males without any external damage were collected from the breeding box and kept in groups for 48 h in the dark, in boxes with water and food. Females were not used to avoid any behavioral variability due to their reproductive cycle.

2.2. Experimental procedure

The experimental setup was made up of a circular arena limited by a black polyethylene ring (diameter: 100 cm, height: 20 cm). To prevent cockroaches from escaping, the inner surface of the ring was covered by an electric fence (alternation of positively and negatively charged aluminum layers 19 V; 0.2 A). Lightning was made of four lamp bulbs (Philips ambiance Pro, 20 W) placed above the setup and providing homogeneous illumination intensity at ground level (355 ± 5 lx). Two shelters made of transparent Plexiglas discs (diameter: 15 cm) were hanged by three nylon threads (diameter: 0.3 mm) and positioned symmetrically with reference to the centre of the arena. The centre of each disc was located 23 cm from the edge of the arena and 3 cm above the floor arena. To obtain different luminosity levels under the shelters, we covered each shelter with red color filter film (Rosco color filter, E-Color #19: Fire). A dark shelter was covered by two layers of color filter (ground luminosity: 75 ± 5 lx) and a light shelter covered by only one layer (100 ± 5 lx). The choice of red light shelters was motivated by the following observations: (1) *P. americana* cockroaches are likely to stop as they run through a shadowed area (Meyer et al., 1981) and (2) cockroaches perceive red light as darkness due to the lack of red light-sensitive photo-receptors in their compound eye (Mote and Goldsmith, 1970; Bell and Adiyodi, 1982). In addition, color filters allow observing the behavior of cockroach under a shelter. To avoid possible bias in the shelter selection due to visual landmarks, the whole experimental setup was surrounded by opaque sheets. The floor of the arena was covered by a white paper sheet (120 g/m^2). Between successive experiments, the arena floor was renewed and both shelters were randomly inverted and cleaned with denatured ethanol (97.1% of ethanol + 2.9% of ether). The temperature in the setup was maintained at 20 °C ± 1.

At the beginning of each trial, a cockroach was introduced in the centre of the arena. Each cockroach was tested individually and was used only once. Each trial lasted 3 h and was recorded with a camera centred on the arena (Fire-I Digital camera, Unibrain). A total of 32 cockroaches were observed.

2.3. Data collection and analysis

2.3.1. Data collection

During a 3-h period, we automatically monitored the spatial position of cockroaches (sampling rate: 1/30 s) using a tracking software (Swisstrack: Correll et al., 2006). For each cockroach, the time spent (i.e. staying time) in one of the three zones of the arena (light or dark shelter, outside shelters) was defined as the delay between the entrance and the exit of the individual from this zone. For the analysis, a cockroach either resting or moving under a shelter was considered to be under a shelter.

2.3.2. Data analysis

Experimental data were tested for deviance from normality using the Kolmogorov–Smirnov test. When the normality and homogeneity of the variance assumption were met, we carried out parametric tests; otherwise, we performed corresponding non-parametric tests. Statistical tests were two-tailed and were conducted with GraphPad Instat® for Windows, except for the Kolmogorov–Smirnov two-sample test and Logrank test, which were conducted following Zar (1999). Survival curves of resting times were fitted using non-linear least-square regressions performed with GraphPad Prism® and R version 2.5.1. The parameters obtained from these regressions were subsequently implemented in a numerical model (see below). The significance of the statistical tests was fixed to $a = 0.05$ (Zar, 1999).

3. Results

3.1. Settlement under both shelters

By pooling data for the 32 observed individuals, we show that the percentage of cockroaches under shelters increased slowly over time to reach a plateau value of around 22% (Fig. 1). This value corresponded to seven experiments in which the cockroach individuals were located under one of the shelters (4 under the dark and 3 under the light one) at the end of the observation period ($t = 10{,}800$ s).

Assuming that cockroaches do not have any preference for staying under a shelter in comparison to the arena (i.e. random distribution), the theoretical probability (P_{th}) to observe an individual under a shelter is given by the ratio between the summed shelters areas of shelters and the total area of the arena:

$$P_{th} = \frac{2\pi r^2}{\pi R^2} = 0.045 \qquad (1)$$

where r and R are the radius of a shelter and an arena, respectively.

Assuming that cockroaches did not change their behavior when walking under a shelter, the theoretical probability of obtaining seven or more experiments ending with a cockroach under a

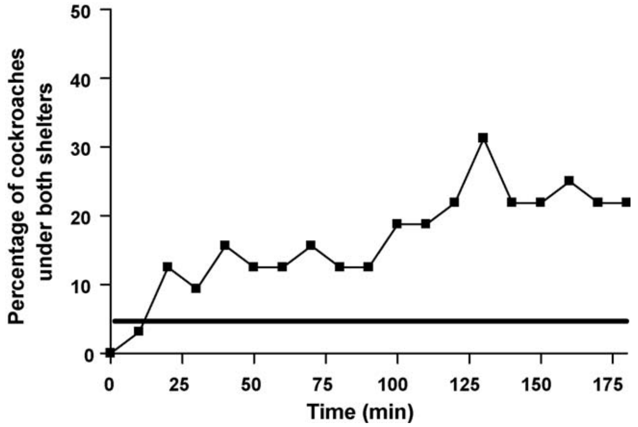

Fig. 1. Temporal evolution of the percentage of isolated individuals staying under either shelter (all individual data were pooled; $N = 32$ individuals). The horizontal line corresponds to a randomness distribution of individuals.

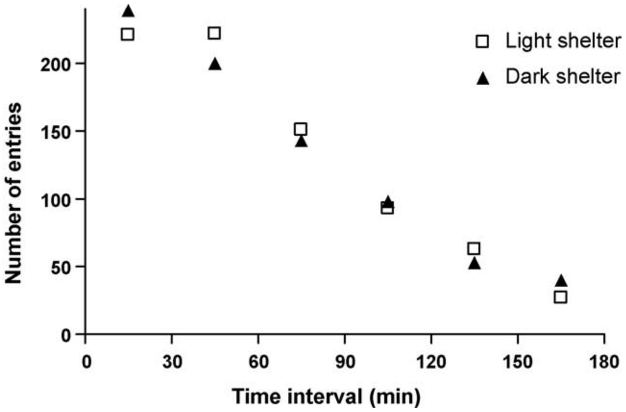

Fig. 3. Temporal evolution of the total number of entries for each 30-min interval under the dark and under the light shelter ($N = 32$, total number of entries = 1554).

shelter (22% of the 32 tested individuals) is less than 0.0005, according to a binomial distribution. The observed percentage of cockroaches found under shelters was thus higher than expected from a spatial distribution not sensitive to environmental cues. This shows that cockroaches perceived shelters as preferred resting sites in comparison to the rest of the arena. While the area of the shelters represented 4.5% of the total area, the mean time spent per individual under both shelters (mean ± SD: 1778 ± 2509 s; $N = 32$) equaled 20% of the total time of experiment (10,800 s).

3.2. *Resting under shelter according to luminosity (dark or light)*

For the whole duration of the experiment, a cockroach was equally likely to enter in the dark shelter or in the light one (Wilcoxon matched-pairs: $P = 0.53$; $N = 32$ pairs). The average numbers of entries into the dark and the light shelter were similar (mean ± SD: dark: 24.0 ± 19.1, $N = 772$; light: 24.3 ± 19.4, $N = 782$). The total number of entries per individual under the dark and under the light shelter was correlated (Fig. 2, Spearman correlation: $r = 0.88$, $F = 79.96$, $P < 0.0001$). This indicates that individuals differed in their motility but did not show any preference in entering one of the shelters.

The total number of entries under the light or the dark shelter per 30-min time interval decreased linearly over time (Fig. 3, light shelter: linear regression, $F = 100.00$, df = 4, $P < 0.001$, $R^2 = 0.96$; dark shelter: linear regression, $F = 189.6$, df = 4, $P < 0.0005$, $R^2 = 0.98$). The slopes of the regression lines (for the light: βlight = −0.69; for the dark: βdark = −0.70; test for comparison of two slopes: $F = 0.017$, df = 8, $P = 0.9$) and the elevations (comparing intercept: $F = 0.006$, df = 9, $P = 0.94$) did not differ significantly. These results indicate that the number of entries decreased overtime similarly for both shelters.

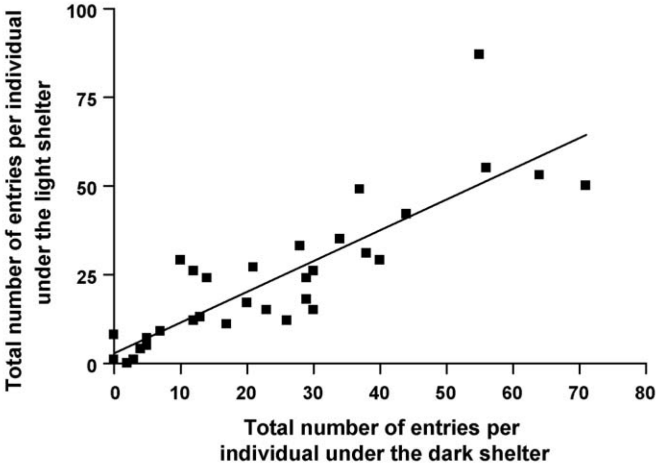

Fig. 2. For each individual ($N = 32$), correlation between the total number of entries under the dark and under the light shelter. $y = 0.867x + 2.879$ ($P < 0.0001$, $R^2 = 0.73$).

The mean resting time per visit (all data pooled) under the dark shelter was longer than under the light one (dark = 42.6 ± 373.1 s ($N = 772$) and light = 28.8 ± 366.3 s ($N = 782$)). Cockroaches modulated their resting time under a shelter depending on its quality. This will be further detailed through the analysis of the individual decision rules.

3.3. *Individual decision rules*

A cockroach could be located either under a dark or a light shelter or outside shelters, four transition probabilities can describe the transitions between these three zones (Fig. 4). We defined L_D and L_L as the probabilities per unit of time (s^{-1}) of leaving the dark or the light shelter respectively; J_D and J_L are the probabilities per unit of time of joining the dark or the light shelter respectively.

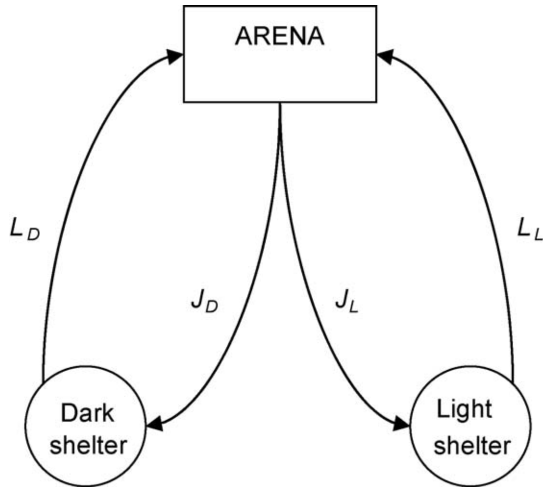

Fig. 4. Flowchart illustrating the transition probabilities between the arena and the shelters; J_D and J_L are respectively the probability per unit of time of joining the dark or the light shelter and L_D and L_L the probability per time unit of leaving them.

3.3.1. Probability per time unit of joining a shelter

The estimation of the probability of leaving each zone of the arena (shelters and outside shelters) is based on the survival curves of the time spent in each zone. The survival curve corresponds to the fraction of individual (f) that is still in the compartment after a specified time (t). At time $t = 0$, $f = 1$. The individual being isolated, the decreased rate of this fraction (the slope or the derivative of the survival curve) is proportional to this fraction f and to the individual probability of leaving at this time ($J(t)$):

$$\frac{\mathrm{d}f}{\mathrm{d}t} = -J(t)\,f \tag{2a}$$

$$\ln f = -\int_0^t J(\tau)\,\mathrm{d}\tau \tag{2b}$$

We aim at determining the individual probability of leaving the arena (i.e. joining a shelter) for cockroaches moving in the arena. We measured the time spent by all cockroaches ($N = 32$) in the arena between two successive visits from either shelter. The log-linear plots of the survival curves of the staying times are characterized by a fast decay followed by a slow decay (see Fig. 5). This result indicates that the individual probability of leaving $J(t)$ decreased with the time spent outside the shelters (in the rest of the arena). A classical form of such decrease is

$$J(t) = \frac{\alpha}{\chi^{\beta} + t^{\beta}} \tag{2c}$$

with α, β and χ being constant values.

The first hypothesis is to assume that $\beta = 1$. In this case, the probability of leaving $J(t)$ is inversely proportional to the time (t) spent outside the shelters and for $t = 0$, $J(0) = \alpha/\chi$.

With such hypothesis, Eq. (2b) is

$$\ln f = -\alpha \ln \frac{\chi + t}{\chi} \tag{2d}$$

or

$$f = \frac{1}{(1 + t/\chi)^{\alpha}} \tag{2e}$$

The second hypothesis ($\beta > 1$) was not tested. Indeed, with such value of β, f exhibits a pathological behavior; a fraction of the population can remain irreversibly trapped outside the shelters.

The best fit of experimental data was obtained with $\alpha = 1.09$ and $\chi = 43.10$ (Logrank test: $\chi^2 = 0.18$, df = 1, $N = 377$, $P > 0.05$, $R^2 = 0.99$). Based on experimental observations (see previous Section 3.2), there was no difference in the number of visits under a light or a dark shelter, thus $J_L = J_D$. Consequently, the individual probability $J(t)$ of joining one of the shelter per time unit is given by

$$J_D(t) = J_L(t) = \frac{J(t)}{2} = \frac{\alpha}{2(\chi + t)} \tag{2f}$$

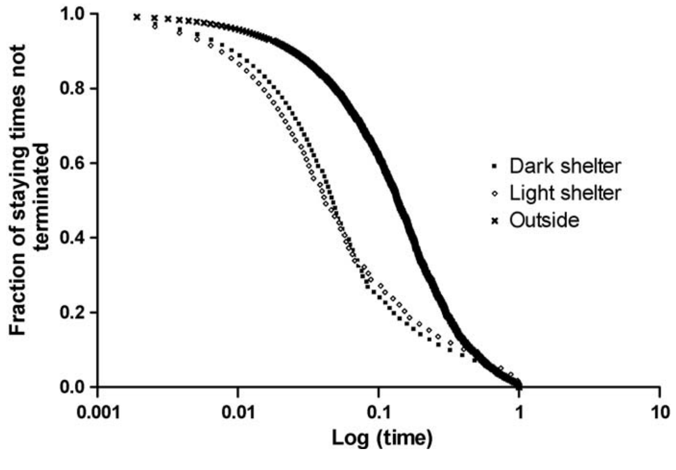

Fig. 5. Experimental survival curves of the staying times spent under dark shelter (square), light shelter (lozenge) and outside shelter (cross).

3.3.2. Probability per time unit of leaving the shelter

To determine the influence of shelter luminosity on the individual probability of leaving a shelter per unit of time depending on its luminosity, we pooled staying times under each shelter for all individuals and followed the same procedure as described above. For both conditions (dark and light shelter), the corresponding survival curves were qualitatively similar to the one of staying outside the shelters (see previously). We observed the same abrupt decrease followed by a slow decay in these two curves. This suggests that the probability of leaving per unit of time $L(t)$ is high for short staying times and decreases with the time already spent under the shelter (Fig. 5). As for the probability of leaving the arena, the fraction still under shelters is well fitted with Eq. (2e) and the probability of leaving the shelter per unit of time is given by equation:

$$L_L(t) = \frac{\alpha_L}{\chi_L + t}; \quad L_D(t) = \frac{\alpha_D}{\chi_D + t} \tag{2g}$$

The best fitting for the light shelter was obtained with $\alpha_L = 0.87$ and $\chi_L = 2$ (Logrank test: $\chi^2 = 0.58$, df = 1, $N = 59$, $P > 0.05$, $R^2 = 0.98$) and for the dark with $\alpha_D = 0.9$ and $\chi_D = 3$ (Logrank test: $\chi^2 = 0.01$, df = 1, $N = 71$, $P > 0.05$, $R^2 = 0.94$).

It is worth noting that these survival curves are not a by-product of pooling all individual data. For each individual survival curve drawn for cockroaches having more than 10 staying times recorded (22 individuals corresponding to 90% of the total staying times observed), the best fit was also obtained by Eq. (2e) (for all individual, $R^2 > 0.88$). Moreover, there was no correlation between the duration of a resting time and its rank of appearance during experiments (for all individuals, Spearman rank correlation test: $-0.241 < r < 0.368$, $P > 0.05$). This result means that the probability to find a short (respectively a long) resting time is constant during the experiment.

Finally, we compared the probabilities of leaving either the dark $L_D(t)$ or the light $L_L(t)$ shelter. The experimental survival curves of both shelters were linearized by a logarithmic transformation (light shelter: linear regression, $F = 2013.69$, df = 69, $P < 0.0001$, $R^2 = 0.97$; dark shelter: linear regression, $F = 1816.36$, df = 57, $P < 0.0001$, $R^2 = 0.97$). The probability of leaving was significantly larger for the light than for the dark shelter as demonstrated by the steeper slope of the regression line for the dark site than for the lighter one (test for comparison two slopes: $t_{0.05(2),\ 2398} = 7.55$, df = 124; $\beta_{\text{dark}} = -0.75$; $\beta_{\text{light}} = -0.96$, $P < 0.05$).

3.4. Model

3.4.1. Model for individual decision-making

We built a numerical model of individual decision-making (see Eqs. (2f) and (2g)) implementing the behavioral rules derived from our experimental data. In this model, three compartments were considered: light or dark shelter and the rest of the arena. There was no direct transition between shelters. At the beginning of a simulation run, a cockroach was initialized outside shelters. At each time step, the individual probability (per unit of time) of joining a shelter was given by Eq. (2f) or the probability of leaving it depending on its luminosity was given by Eq. (2g). In simulations, the experimental timescale was preserved (t = 10,800 s), and we applied time steps of 1 cycle/s. A total of 1000 simulations of 32 individuals were performed.

Table 1

Comparison between experimental and theoretical data analyses; based on the mean of 1000 simulated groups of 32 individuals.

		Experimental	Theoretical
Mean fraction of individuals at t = 180 min	Light	0.093	0.0511 ± 0.040
	Dark	0.125	0.0721 ± 0.047
	Outside	0.780	0.876 ± 0.061
Mean number of entries per individual	Light	24.30	22.83 ± 2.014
	Dark	24.00	23.10 ± 2.011
	Outside	49.125	46.476 ± 3.841
Mean staying time per visit (s, ±SD)	Light	28.81	24.617 ± 8.476
	Dark	42.62	34.115 ± 10.085
	Outside	184.61	205.020 ± 18.850

The experimental and theoretical results are summarized in Table 1. Overall, there was a good agreement between both data sets (Fig. 6a–d).

3.4.2. *Interindividual variability*

From our experimental data, we showed that every individual follows the same decision rule (probability of joining or leaving a shelter). However, the resting time and the number of entries showed a relatively important variability between the 32 cockroaches tested (see Figs. 2 and 7). For instance, the total number of entries under a shelter varied between 1 and 142 and the total resting time under the shelters ranged between 14 and 9214 s. We examine whether this interindividual variability could be under the unique influence of the t^{-1} power law without considering any intrinsic difference between individuals in their probability of leaving or joining shelters. In other words, the variability among cockroaches could originate from the same behavioral rule: the t^{-1} power law. This hypothesis was validated by comparing our experimental results with the outputs of simulations assuming the absence of interindividual variability (i.e. all individuals behaved and responded in the same way to shelter's quality). We run the numerical model implemented with the same parameter values and tested 32,000 theoretical individuals. From the simulations, we obtained a high variability between individuals comparable to the observed one. Indeed, the total number of entries per individual did not differ between theoretical and experimental data sets (Kolmogorov–Smirnov test: KS = 0.31, $P > 0.05$, Fig. 7).

4. Discussion

In this study, we examined how the individual sensitivity to environmental factors shaped the decision to select a shelter in absence of any social influence. We quantified the total time spent under a shelter by isolated cockroaches and how this time depended on the probabilities of entering and leaving shelters according to their quality. We showed that cockroaches were unable to discriminate site quality from a long distance but that they modulated their resting time depending on shelters properties. In addition, our results indicate that the probability of leaving a shelter depended upon settlement time. The probability of leaving follows a power law t^{-1} where the variable t corresponded to the time already spent under the shelter. The observed decrease of the number of entries over time is a consequence of the increasing individual probability of being engaged in a long staying time all along the experiment. Each individual was thus able to "self-amplify" its staying time. This trend, observed for every tested cockroach, agrees with results obtained for the urban cockroach: *Blattella germanica* (Jeanson et al., 2005; Jeanson and Deneubourg, 2007). Two factors act concomitantly: (1) the shelter, according to its own quality (e.g. the luminosity), retains the cockroach for long duration, then (2) the power law departure rule enhances the stay of individuals showing longer resting times.

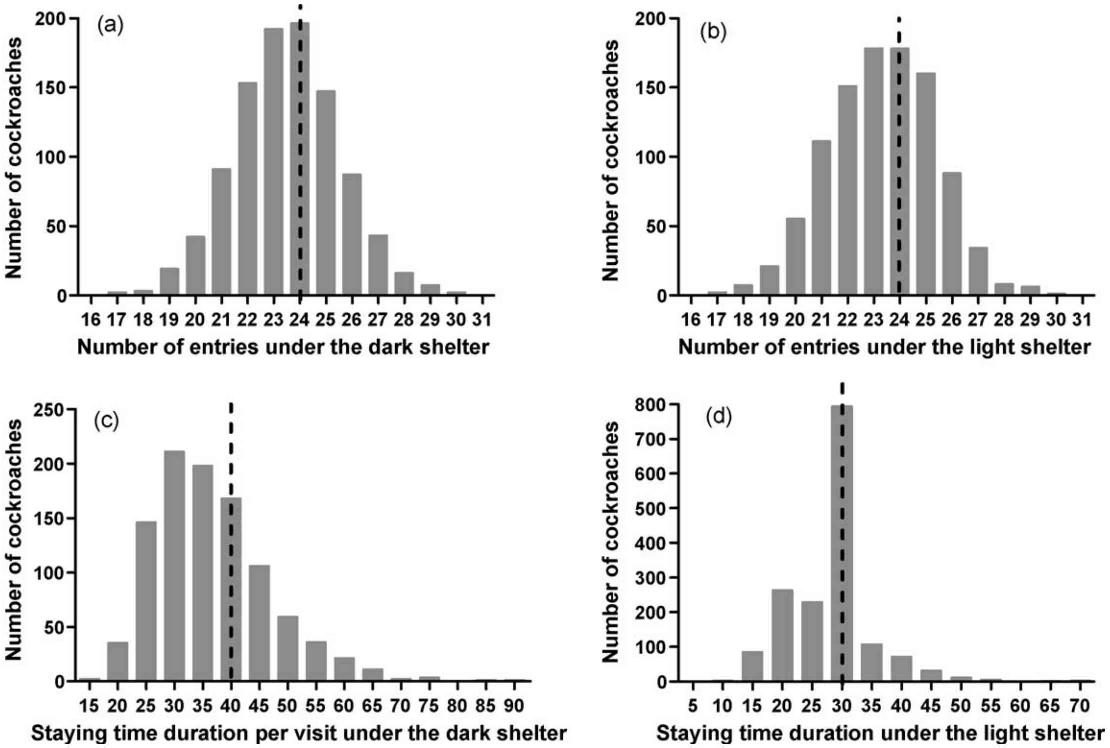

Fig. 6. Comparisons between the theoretical distribution of the number of entries (a and b) and of the staying time duration (c and d) with experimental data: the dotted lines correspond to the mean experimental.

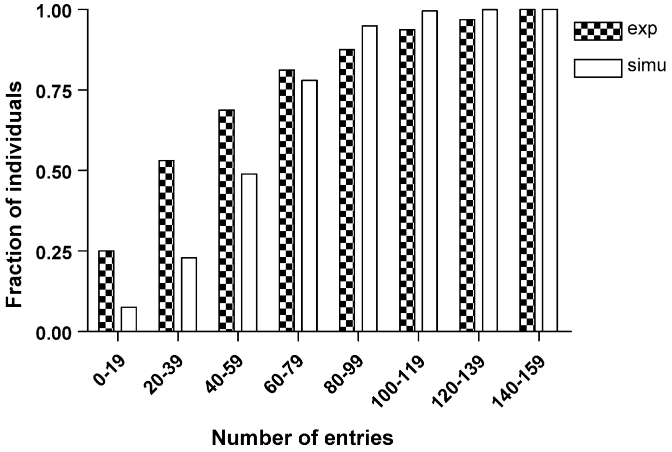

Fig. 7. Comparison of the total number of entries per individual between experimental ($N = 32$) and simulation ($N = 32,000$) data.

From empirical data, we designed a decision algorithm based on the following rules: (1) the probabilities of entering were similar for both shelters; (2) the probabilities of leaving were dependent on shelter quality and staying-time duration. The temporal sequences of staying times per individual did not follow a specific order: short staying times could happen either at the beginning or at the end of experiment. First, simulations showed that these simple behavioral rules were sufficient to reproduce the observed spatio-temporal distribution and staying-time dynamics, without considering a hypothetical comparison between shelters or spatial fidelity expressed by cockroaches. Second, we analyzed quantitative differences among simulated individuals: some cockroaches were characterized by either a low or a high frequency of entries, and by either a low or high total resting time under shelter. However, the population cannot be divided into distinct subgroups since each individual may show both short and long staying times. We do not deny that each individual can be characterized by its own set of behavioral, physiological and morphological parameters rising from its genetic background, age and learning. However, our theoretical analysis shows that the interindividual variability may be largely due to the transition probabilities that follow a power law. In other words, self-amplification, exerted over the probability of leaving, generated a high variation among individuals and can ultimately lead to social differentiation (see Ravary et al., 2007).

These results stress the adaptive value of a t^{-1} power law function ruling the departure of animals from a resting site. This is a particular case of more general question: how does the duration of an activity affect the probability of ending it (and of a new one being started)? Three main types of answers have been reported in living systems. The most common case is that the probability of ending an activity is an increasing function of the time already spent into this activity. This behavior is linked to saturation due to fatigue or satiation (food ingestion in ants, Mailleux et al., 2000). Secondly, some behavior are characterized by a constant probability of ending, such as the individual probability of ants to leave a trail (e.g. Pasteels et al., 1986; Calenbuhr and Deneubourg, 1992; Calenbuhr et al., 1992). In this latter case, the behavior can be adequately characterized by a single time constant and therefore described by an exponential distribution of the activity duration. Thirdly, a few cases in very different biological systems are better described by power laws: the probability of ending an activity decreases with the time already spent into this activity (Bassingthwaighte et al., 1994; Yokoyama et al., 1996). For example, the duration of the inactivity phases and the shift between the active and inactive phase in *Drosophila* species are power law dependent (Cole, 1995; Martin, 2004) and the dwelling time of starved flies on food shows a clear inverse power law distribution (Shimada et al., 1993). In terms of costs and benefits, power law dependent decision rules reflect the trade-off between going on and stopping an activity. The main benefit issued from such rules is to enhance the individual ability to display discriminated behavior that best fit their needs when they live in a heterogeneous environment. Power law functions appear as the core of major biological features (Newman, 2005). Several costs are also related to spatial and task specialization issued from power law decision rules: (1) one individual can fail to discover other more profitable resources; (2) it can be prevented from meeting all its physiological needs —e.g. when they are spatially exclusive (safe resting in a site vs. meeting a sexual partner in another site); and (3) by its persistence in a given location/activity, it become more sensitive to detection by a predator or a competitor.

This paper has highlighted the decision rules that act upon the resting behavior of 1 cockroach. The slight preference to settle longer under the darkest shelter for isolated cockroach contrasts with the highly marked preference for this same site when they are in group. In many gregarious species such as cockroaches, social interactions among group-members drive aggregative behavior of individuals and contribute to resources selection (Bell and Adiyodi, 1982; Chapman, 1998; Costa, 2006). For instance, in another urban cockroach species (*B. germanica*), individuals increase their resting behavior depending on the presence of conspecifics under the shelter (Ame et al., 2004; Jeanson et al., 2005; Jeanson and Deneubourg, 2007). More generally, in group-living animals, the consensual decision about the suitability of a resource should result from the integration of both environmental and public information (Doligez et al., 2004; Dall, 2005). In cockroach, this can be achieved through the use of two complementary processes: (1) a self-amplification (power law), which depends on the preference of an individual for some features of its environment and (2) a collective amplification through the presence of conspecifics (Parrish and Edelstein-Keshet, 1999; Couzin and Krause, 2003). Preliminary results show that this slight preference of *P. americana* individuals to settle longer under a dark shelter is amplified in presence of congeners. Our hypothesis is that the interplay between both individual preferences and social interactions should lead to a clear-cut choice of the dark site by a group.

The next step will be to investigate how interactions among group-members modify individual decision process leading to the formation of a self-organized spatial structure at the collective level. One central question in biology is how collective behavior and social organization can emerge in large systems from individual components differing in their needs, preferences or behaviors (Pasteels and Deneubourg, 1987). Further empirical and theoretical work is also needed to fully understand the physiological and ecological basis underlying the considerable variation in individual behavior that could ultimately lead to their categorization depending on their types or strategies (worker, explorer, etc.) (West-Eberhard, 1989). In this context, cockroach provides an excellent biological model to study the relationship between behavioral modulation and physiology (Goldstein and Camhi, 1991; Libersat and Pflueger, 2004).

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