



# Complex Dynamics Based on a Quorum: Decision-Making Process by Cockroaches in a Patchy Environment

Grégory Sempo, Stéphane Canonge, Claire Detrain & Jean-Louis Deneubourg

Unit of Social Ecology (CP231), Université libre de Bruxelles, Bruxelles, Belgium

## Correspondence

Sempo Grégory, Unit of Social Ecology (CP231), Université libre de Bruxelles, 50 Avenue F.D. Roosevelt, 1050 Bruxelles, Belgium.  
E-mail: gsempo@ulb.ac.be

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## Abstract

In the absence of complex communication and a global knowledge of the environment, cockroaches are able to assess the availability of resources and to reach a consensual decision: the group aggregates in a single resting site. We show that the aggregation dynamics and the collective shelter selection of cockroaches are influenced by their social context as, unlike single individuals, groups of cockroaches are more likely to respond to environmental heterogeneities. The decision of individuals to stay under a shelter relies on the modulation of their resting time, according to the perception of two local cues: (1) the shelters luminosity and (2) the number of congeners. This study on the cockroach species *Periplaneta americana* highlights a shelter-selection mechanism based on an amplification process resulting from the interactions between congeners. This mechanism leads to complex spatiotemporal aggregation dynamics characterized by transient bimodality, bifurcation patterns (shelter selection) and the existence of a quorum size in the settlement behaviour of the cockroaches. Finally, we discuss the generic aspect for other gregarious species of the collective decision-making process demonstrated for cockroaches.

## Introduction

Aggregation occurs in many biological systems: from bacteria to vertebrates (Parrish & Edelstein-Keshet 1999; Krause & Ruxton 2002; Ben Jacob et al. 2004). Among ultimate causes of living in groups, costs and benefits of aggregating in space and time are extensively described in the literature (Allee 1926; Hamilton 1971; Parrish 1989; Krause 1994; Choe & Crespi 1997; Watt & Chapman 1998; Stephens & Sutherland 1999). Costs to group members involve a sharing of food resources (Giraldeau & Caraco 2000), a higher competition for sexual mates (Moller & Birkhead 1993), or an increased parasitic burden (Van Vuren 1996). However, it also brings several advantages by allowing information transfer between individuals (Dall et al. 2005), promoting cooperation in foraging (Creel & Creel 1995; Vasquez & Kacelnik 2000) or in parental care (Choe & Crespi 1997; Sempo et al.

2006a) and facilitates thermo- and hygroregulation (Heinrich 1981; Ancel et al. 1997; Dambach & Goehlen 1999) or protection against predators (Bertram 1978; Treherne & Foster 1980).

In a patchy environment, the habitat at which aggregation takes place will deeply influence the fitness of the inhabiting species. As the intrinsic quality of the habitat varies in time and space (Orians & Wittenberger 1991), animal species have to select the optimal site and could notably rely on public information that provides a more accurate estimate of habitat quality (Doligez et al. 2004). In this respect, the presence of conspecifics provides a local cue (Boulinier & Danchin 1997; Detrain & Deneubourg 2009) that can be used by individuals in their 'shared information' strategy (i.e. social attraction: Stamps 1988; Reed & Dobson 1993; Muller 1998; Conradt & Roper 2005). The rate of encounters or any activity by-product testifying the presence of

individuals sharing similar preferences, notably for food and shelter features, indicates the adequacy and the quality of a habitat (Danchin et al. 2004; Devigne et al. 2004; Fletcher 2007; Sempo et al. 2006b). In this respect, information provided to gregarious animals by their conspecifics is an important cue for individuals before deciding whether to stay on a site or not.

While the functional value of group-living in a common habitat has been widely discussed, only a few studies have extended beyond the mere description of spatial patterns and looked into the proximal causes and the behavioural mechanisms governing animals' aggregation. The more advanced studies in this field have been carried out on social amoebae (Kessin 2001), on fish (Krause & Tegeder 1994; Parrish & Hamner 1997) and on cockroach (Amé et al. 2006a). In most cases, aggregation is an active process resulting from directed movements of individuals towards two types of stimuli. The first type of stimuli originate from the environment and consist of local heterogeneities (light gradient, soil irregularities, temperature gradient, etc.) (Fraenkel & Gunn 1961): they can be used as cues by each individual for assessing the potential quality of a location and for eliciting a directed movement or an increased resting time. In this case, the final aggregation pattern results from the summation of individual behavioural responses to environmental cues without assuming that social interactions are involved. The aggregation pattern that emerges is independent from the number of group members, as well as from the initial spatial localization of individuals (Camazine et al. 2001). Moreover, the removal of the external cue results in the dispersion of the cluster members.

The second type of aggregating stimuli, on which this study is focused, occurs in the presence of congeners, where each individual can become an attractor for the other ones. This inter-individual attraction is tightly related to the presence of congeners and can induce, in relation with environmental external cues, the emergence of adaptive group behaviour (Parrish & Hamner 1997). Such mutual attraction, and the cluster formation that ensues, has been reported in the majority of group-living animals (Krause & Ruxton 2002; Costa 2006). Concerning gregarious insects, it has been demonstrated that aggregation patterns often result from the modulation of the resting time as a function of the cluster size (Amé et al. 2004, 2006b; Depickère et al. 2004; Jeanson et al. 2004; Halloy et al. 2007; Jeanson & Deneubourg 2007). In these latter cases, the aggregation pattern is a by-product of the local

interactions of an individual with its congeners according to environmental characteristics, without any knowledge of the global pattern (Dambach & Goehlen 1999; Camazine et al. 2001; Theraulaz et al. 2002). To aggregate at the same place, individuals have to attain a consensus decision without direct comparison of the different aggregation sites and with only local communication. This consensus assumes that the decision is taken independently of individual identities or social status of group members. This shared decision could be based on a minimum number of individuals, or quorum, taking a particular action (Conradt & Roper 2005). This density-dependent mechanism implies that individuals are able to sense whether the quorum has been reached or not through the estimation of individual density. The existence of quorum, originally developed from studies on bacterial cells (Diggle et al. 2007), has been mainly described for behavioural changes in locusts (Collett et al. 1998) and in social insects (Seeley & Visscher 2004; Pratt 2008).

As each group member is sensitive to a variety of environmental and social stimuli, the understanding of emergent spatial patterns requires a detailed analysis of individual behavioural rules (Deneubourg & Goss 1989; Bonabeau et al. 1997; Detrain & Deneubourg 2006; Sumpter 2006). Therefore, one should investigate whether and how the combined effects of all these cues act as positive or negative feedbacks in the aggregation process and lead to the emergence of complex collective patterns. In particular, one should relate the spatial patterns of one species to the properties of its social interactions, which may act over different spatiotemporal scales depending on whether chemical, visual, acoustical and/or tactile communication is involved.

In this context, our study on the gregarious cockroach *Periplaneta americana* aimed to investigate its aggregation behaviour in a patchy environment deprived of any landmarks with the exception of two identical resting sites. This investigation falls within the scope of the nest/shelter selection by group-living animals (Conradt & Roper 2005).

Without any modification of the environment, we aimed to highlight the contribution of social interactions in the emergence of collective aggregation patterns. Like most urban cockroach species, *P. americana* is described as gregarious (Cornwell 1968; Bell & Adiyodi 1982; Leoncini & Rivault 2005). Individuals alternate diurnal phases of aggregation inside shelters and nocturnal phases of dispersion to explore and forage for food resources (Appel 1995). During the day, *P. americana* individuals are

likely to stop in shadowed areas what imply that they increase their resting time in these places (Meyer et al. 1981). Knowing that the resting time of a *P. americana* individual is tuned by its perception of shadow, as well as by the presence of congeners (Leoncini & Rivault 2005; Saïd et al. 2005; Canonge et al. 2009), our study analysed the synergies and the responses that emerges at the group level from the combined effect of environment patchiness and social cues. Based on the nonlinear response of individuals to congeners, a previous study has shown how collective decision-making could lead to optimal group formation from observation performed only on steady-states obtained at the end of the aggregation process (Amé et al. 2006a). In this theoretical context, we do not limit our observation to the final aggregation pattern and, by taking into account the whole spatio-temporal evolution of clusters, investigated in detail how group size determines the dynamics, as well as the stability, of the aggregation process. Moreover, we will examine the existence of quorum, its size according to the population size and how it affects the aggregation dynamic.

## Methods

### Rearing of Cockroaches

Adult males of *Periplaneta americana* were reared in transparent boxes (length: 80 cm; width: 40 cm; height: 100 cm) containing shelters (cardboard cylinders; length: 30 cm, diameter: 5 cm). Tested cockroaches all belonged to a strain breed in our laboratory since more than 5 yrs. They had *ad libitum* access to water and food pellets (Tom & Co™ dog food, Aniserco S. A., Brussels, Belgium). Cockroaches were kept at a temperature of  $25 \pm 1^\circ\text{C}$  and under a 12 h:12 h light:dark cycle.

### Experimental Setup

The experimental setup consisted of a circular arena delimited by a black polyethylene ring (exterior diameter: 100 cm, height: 20 cm, thickness: 1 cm). To prevent cockroaches from escaping, the inner surface of the experimental arena was covered by an electric fence composed of alternating positively and negatively charged black aluminium layers (19 V, 0.2 A). The ground of the experimental arena was covered with a white paper sheet ( $120 \text{ g/m}^2$ ) and replaced between each experiment. Illumination was ensured by four lamp bulbs centred on the experimental arena (20 Ws; Philips Ambiance Pro, Philips

Belgium NV, Brussels, Belgium) and providing  $355 \pm 5 \text{ lux}$  at the ground level.

Two shelters consisting of Plexiglas discs (diameter: 15 cm) were suspended by means of nylon threads (diameter: 0.3 mm) above the arena and positioned symmetrically to its centre. Their size allowed them to contain up to 35 cockroaches without any overcrowding. The centre of each disc was then localized at 23 cm from the edge of the arena and at 3 cm above the ground. The whole setup was surrounded by an opaque white enclosure to prevent the cockroaches perceiving visual landmarks outside the experimental arena. In addition, the angular position of each pair of shelters was randomized between replicates. Discs were cleaned with denatured alcohol (97.1% ethanol + 2.9% ether) between each experiment. To decrease the luminosity under the discs, two layers of a red filter ( $75 \pm 5 \text{ lux}$ ; Rosco colour filter, E-Colour #019: Fire, Roscolab Ltd., London, UK) were used to cover them. The choice of such a red-light shelter was driven by the two following observations: (1) *P. americana* stop running as soon as they enter a shadowed area (Meyer et al. 1981) and (2) *P. americana* perceive an area illuminated by red light as a shadow because of the lack of red-light-sensitive photoreceptors in their compound eye (Mote & Goldsmith 1970). The temperature in the experimental setup was maintained at  $20 \pm 1^\circ\text{C}$ .

### Experimental Procedure

Two days before the experiments, adult males of *P. americana* (1, 10, 16 or 30 males depending of the experiment, see below) were taken from the rearing box and isolated 48 h in total darkness in a smaller box (length: 36 cm; width: 24 cm; height: 14 cm) containing water, food pellets (Tom & Co™ dog food) and shelters (cardboard cylinders: length 30 cm, diameter 5 cm). Animals with any external damage (e.g. missing antennal segments or leg parts) were discarded. Following this isolation period, awaked cockroaches were introduced by emptying the smaller box in the centre of the experimental arena. From this introduction and during a 180-min period, the number of individuals under each shelters was counted every 10 min (19 observations) using a camera placed between lamps and centred on the arena.

### Data Analysis

The deviation from a binomial distribution is used to highlight an amplification process in the spatial distribution of individuals. Data from all the

experiments were tested for any deviance from normality using the Kolmogorov–Smirnov test. When normality conditions were met, we carried out parametric tests; otherwise, we performed corresponding nonparametric tests. To satisfy normality, one-, two- and three-way analyses of variance (ANOVA) with repeated measures were performed on arcsine-transformed proportions (Zar 1999). The observation type (TIME) was the within-subject factor (dependent factor), while shelter type (SHELTER) and/or the population size (POPULATION SIZE) were the between-subject factors. To highlight a plateau in aggregation dynamics, repeated methods of contrasts were used for comparisons of all time step values against the size of the cluster observed at  $t = 180$  min (simple contrast).

All  $p$  values were two-tailed and means are provided with  $\pm 1$  SE. All calculations were carried out using SPSS 14.0 software (SPSS Inc., Paris, France). The significance of the statistical tests was fixed to  $\alpha = 0.05$ .

## Results

### The Influence of Population Size on the Aggregation Dynamics of Cockroaches

The lower light intensity under the two shelters creates heterogeneities within the experimental arena, which are perceived by cockroaches as resting sites and favour their aggregation. Indeed, after 180 min, populations of 10, 16 and 30 cockroaches show densities under shelters that are greater than the density expected in the case of random distribution of individuals in the arena (Table 1). Unexpectedly, cockroaches seem to react differently to light heterogeneities when tested in isolation or with a group of congeners. Experiments with an isolated cockroach do not show such a preference for resting under the shelters. The results show that their presence rate per unit area did not differ from the value expected for a random distribution of the individuals (Table 1). This shows that because of the influence of congeners, unlike single individuals, groups of

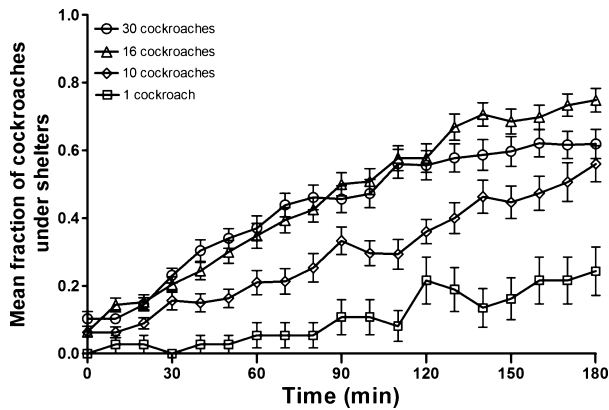
cockroaches are more likely to respond to environmental heterogeneities and to use the shelter as a resting site.

As regards the aggregation dynamics, our results show that the fraction of the cockroach population under the two shelters changes over time and is significantly influenced by the population size (1, 10, 16 or 30 cockroaches; Fig. 1). When analysing the aggregation dynamics separately, we found out that the fraction of the population under shelters increases linearly with time for the four tested population sizes (Fig. 1. Linear regression for one cockroach:  $F_{1,701} = 45.42$ ,  $p < 0.0001$ ; for 10 cockroaches:  $F_{1,568} = 286.8$ ,  $p < 0.0001$ ; for 16 cockroaches:  $F_{1,568} = 45.42$ ,  $p < 0.0001$ ; for 30 cockroaches:  $F_{1,473} = 814.9$ ,  $p < 0.0001$ ). This linearity shows that we are still in the growth phase of the aggregation dynamics even after 180 min of the experiment. As a result of the finite size of the cockroach population, these dynamics should ultimately lead, on longer time scale, to a stabilization of the sheltered population (i.e. a plateau value). Nevertheless, despite the linear trend observed for the four conditions, the aggregation dynamics of 30 cockroaches differ from the others by the occurrence of a plateau at the very end of the experiment. Indeed, from the 150th minute, the mean fraction of cockroaches under shelters no longer varied statistically (one-way repeated measure ANOVA on arcsine-transformed proportions:  $F_{18,522} = 56.7$ ,  $p < 0.0001$ . Simple contrast methods:  $p > 0.05$  only for pairwise comparisons between  $t = 180$  min and all time step values since  $t = 150$ ).

We then compared the slope of the four aggregation dynamics for  $\leq 120$  min to only take the growing phase in account. Our results show that the aggregation rate significantly differs among the four population sizes (Fig. 1; multiple regression analysis:  $F_{3,1578} = 33.6$ ,  $p < 0.001$ ) and shows a trend for larger populations (16 or 30 cockroaches) to aggregate more quickly. However, paired comparisons show that this difference is significant for all comparisons, except when comparing the dynamics of cockroach

Condition	Cockroach density under the two shelters at $t = 180$ min (mean no. individuals/cm <sup>2</sup> $\pm$ SD)		
	Observed	Random distribution	Wilcoxon matched-pairs sigend-ranks test ( $p$ -value)
1 cockroach ( $n = 37$ )	0.0007 $\pm$ 0.0012	0.0001	>0.05
10 cockroaches ( $n = 30$ )	0.0158 $\pm$ 0.0082	0.001	<0.0001
16 cockroaches ( $n = 30$ )	0.0339 $\pm$ 0.0086	0.002	<0.0001
30 cockroaches ( $n = 25$ )	0.0525 $\pm$ 0.0183	0.004	<0.0001

**Table 1:** Comparison between the observed mean density of cockroaches under shelters at  $t = 180$  min and the density expected in case of random distribution of individuals in the experimental arena



**Fig. 1:** Change over time of the fraction of the total population of cockroaches under shelters (mean ± 95% confidence interval) in experiments with 1 (square, 37 replicates, regression line:  $y = 0.001x - 0.021$ ), 10 (diamond, 30 replicates, regression line:  $y = 0.003x + 0.043$ ), 16 (triangle, 30 replicates, regression line:  $y = 0.004x + 0.101$ ) or 30 cockroaches (circle, 25 replicates, regression line:  $y = 0.003x + 0.153$ ).

presence under shelters of larger populations (Fig. 1. Tukey *post hoc* test:  $p > 0.05$  for comparisons between populations of 16 and 30 individuals;  $p < 0.05$  for all other pairwise comparisons between 1, 10, 16 or 30 individuals).

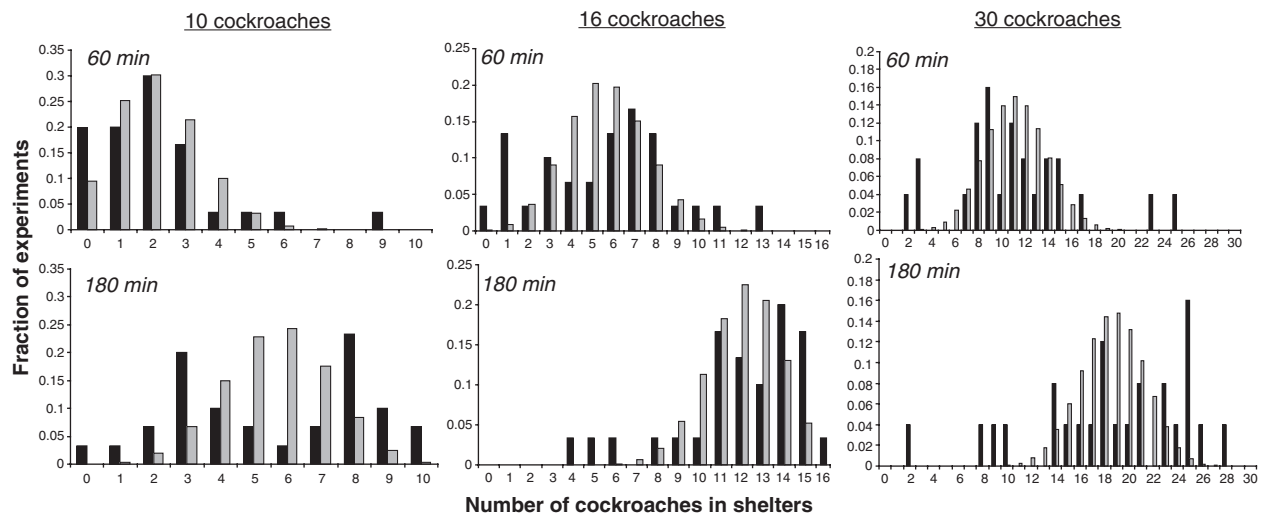
One may wonder whether, and to what extent, social interactions are responsible for the group-level pattern of shelter occupancy. To address this question, for populations of 10, 16 and 30 cockroaches, the experimental distributions of the total number of individuals under shelters after 60 and 180 min were compared with expected distributions (it was

assumed that individuals did not influence each other). The expected distributions were calculated from the binomial function:

$$P(N, n) = \frac{N!}{n!(N - n)!} q^n (1 - q)^{N - n} \quad (1)$$

where  $N$  is the total number of individuals in the experimental setup,  $n$  is the total number of individuals settled under shelters,  $q$  is the probability of one cockroach being found under a shelter and is given by the average fraction of individuals that were observed under shelters after 60 or 180 min of experiment.

After 60 min, the frequency distributions of the numbers of individuals observed under shelters did not differ from the corresponding expected distributions for populations of 10 and 30 cockroaches (Fig. 2. Chi-square goodness of fit test: experimental vs. binomial distribution (see Eq. 1). For 10 cockroaches:  $\chi^2_{0.05,2} = 4.07$ ,  $p > 0.05$ ; for 30 cockroaches:  $\chi^2_{0.05,2} = 4.64$ ,  $p > 0.05$ ). For cockroach groups of intermediate size (16 individuals), the observed frequency distribution of sheltered individuals significantly differs from the expected one (chi-square goodness of fit test: experimental vs. binomial distribution; for 16 cockroaches:  $\chi^2_{0.05,3} = 20.55$ ,  $p < 0.001$ ), by departing from a binomial distribution and showing a ‘bimodal’ shape. These results show that, in a large number of the experiments, a higher number of individuals were found under shelters in comparison with expected results. In contrast, in some experiments the aggregation process had not yet begun by



**Fig. 2:** Frequency distributions of expected (grey stack) and experimental (black stack) numbers of individuals under shelters for 10, 16 and 30 cockroaches. At 60 min,  $q = 0.21$ ,  $q = 0.35$ ,  $q = 0.37$  for 10, 16 and 30 cockroaches respectively. At 180 min,  $q = 0.56$ ,  $q = 0.75$ ,  $q = 0.62$  for 10, 16 and 30 cockroaches respectively (Eq. 1).

the time the recordings were taken. After 180 min, the experimental distributions of sheltered individuals did not fit the expected ones, regardless of the size of cockroach population [Fig. 2; chi-square goodness of fit test: experimental vs. binomial distribution (see Eq. 1); for 10 cockroaches:  $\chi^2_{0.05,2} = 23.05$ ,  $p < 0.001$ ; for 16 cockroaches:  $\chi^2_{0.05,4} = 9.56$ ,  $p < 0.05$ ; for 30 cockroaches:  $\chi^2_{0.05,2} = 14.21$ ,  $p < 0.001$ ].

### Collective Selection of One Shelter

For 10, 16 and 30 *P. americana* adult males, there is a progressive aggregation of individuals under the same shelter leading to the collective choice of only one resting site. For these population sizes, we do not observe any preferential selection of one shelter (left or right) which might result from a bias because of heterogeneities in the laboratory environment (Wilcoxon matched-pairs signed-ranks test; for population of 10 cockroaches: 28 pairs,  $p > 0.05$ ; for population of 16 cockroaches: 28 pairs,  $p > 0.05$ ; for population of 30 cockroaches: 23 pairs,  $p > 0.05$ ).

We investigated whether social interactions were involved in the collective selection of a single shelter. To do so, the observed frequency distributions of the number of individuals under each shelter were compared with expected distributions that assume an equal probability (0.5) of each individual being under the left or the right shelter. In other words, distributions that assume that the choice of one cockroach is independent from the previous choices of its congeners. Expected distributions were obtained by using Eq. 2 (binomial distribution) ( $P(n,l)$  in which  $l$  is the number of individuals under the left shelter and  $n$  is the total number of individuals under both shelters)

$$P(n, l) = \frac{n!}{l!(n-l)!} 0.5^n \quad (2)$$

A shelter was considered as being selected by the group, because of the influence of social interactions, when the observed distributions of sheltered individuals differ from the expected ones at a significance level of 0.05.

Table 2 shows that for populations of 10 cockroaches, 60 min is not long enough for the selection of one resting site, as the selection rate is very low. Over time, the occurrence of collective shelter selection tends to increase (Table 2). For larger sized cockroach groups (30 cockroaches), a clear-cut selection of one of the two identical shelters occurs after only 60 min (Table 2). This trend is confirmed after

**Table 2:** For populations of 10, 16 and 30 cockroaches, percentage of experiments with the significant selection [ $P(n,l) < 0.05$ , see eq. (2)] of one shelter at the 60th and 180th minutes

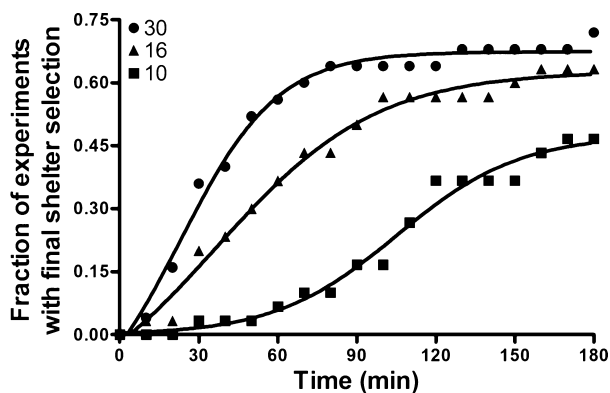
Time (min)	Experiments with the significant selection of one shelter (%)		
	10 cockroaches (30 replicates)	16 cockroaches (30 replicates)	30 cockroaches (25 replicates)
60	3	13	64
180	47	63	72

180 min with 72% of trials characterized by the selection of one shelter (Table 2). One should, however, notice that in 24% of replicates with a population of 30 cockroaches, the aggregation process leads to the concurrent nucleation of aggregates within both shelters and to a long-lasting even distribution of cockroaches under each shelter. As a result of the high percentage of aggregated individuals ( $55 \pm 11\%$ ), the two identical sites are somewhat 'competing' to shelter cockroaches. With 16 cockroaches, there is no concurrent nucleation in both shelters and the aggregation response is intermediate between those obtained with 10 and 30 cockroaches. Indeed, while the selection process is slow for populations of 10 cockroaches (Table 1), at the end of the experiment, the level of selection is higher and close to that observed for 30 cockroaches.

### Influence of Experiment Duration on Selection Stabilization

For each experiment we determined the continuous temporal sequence where the shelter selected at the end (aka. the winning shelter) always contains a more or equal number of individuals than the other one (aka. the losing shelter). By analysing the aggregation pattern every 10 min (total duration: 180 min), we found that the fraction of winner shelters increases as a logistic (or sigmoid) function of time (Fig. 3. Goodness of fit test. For 10 cockroaches,  $R^2 = 0.98$ ,  $p = 0.51$ ; for 16 cockroaches,  $R^2 = 0.99$ ,  $p = 0.09$ ; for 30 cockroaches,  $R^2 = 0.99$ ,  $p = 0.32$ .  $df = 15$  for all conditions). In addition, both the steepness of the curve and the plateau value increase with population size.

Therefore, this result provides information about the stability of the amplification process and the time from which the selection of the shelter is irreversible. In fact, the three populations were markedly different in the time they required for the group to settle down within a shelter and remain there until the end of the



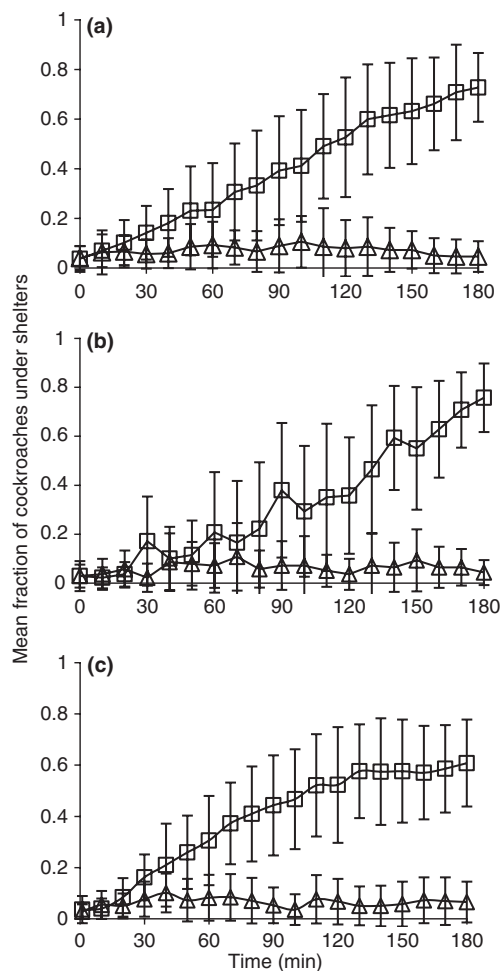
**Fig. 3:** Fraction of experiments having expressed a permanent shelter selection as a function of time for 10 (square), 16 (triangle) or 30 (circle) cockroaches.

experiment. For the experiments ending with shelter selection, the mean duration before the definitive selection of one shelter decreased with the population size; with  $108 \pm 39$ ,  $66 \pm 41$  and  $42 \pm 39$  min for populations of 10, 16 and 30 cockroaches respectively (one-way ANOVA:  $F_{2,48} = 11.2$ ,  $p < 0.0001$ ).

#### Aggregation Dynamics for Experiments with Shelter Selection

By considering only experiments ending with the selection of one shelter, a three-way ANOVA was used to test whether the number of cockroaches under the two types of shelters (selected or unselected shelters, between-subject variable) depends on the observation time (within-subject variable), and/or the population size (10, 16 or 30 cockroaches, between-subject variable). We observed a strong interaction between these three factors on the number of individuals under a shelter (three-way ANOVA with repeated measures on arcsine-transformed proportions. Within-subjects effect,  $\text{TIME} \times \text{SHELTER} \times \text{POPULATION SIZE}$ :  $F_{36,1728} = 2.27$ ,  $p < 0.0001$ ). The main effect on the number of individuals under a shelter is related to the shelter type and not to the population size (three-way ANOVA with repeated measures on arcsine-transformed proportions. Between-subjects effect,  $\text{SHELTER}$ :  $F_{1,96} = 211.5$ ,  $p < 0.0001$ ;  $\text{POPULATION SIZE}$ :  $F_{2,96} = 2.21$ ,  $p = 0.11$ ).

For populations of 10 and 16 cockroaches, the cockroaches under the winning site had not yet reached a plateau value after 3 h of the experiment (Fig. 4a, b. One-way repeated measures ANOVA on arcsine-transformed proportions. For 10 cockroaches:  $F_{18,270} = 24.8$ ,  $p < 0.0001$ ; simple contrast test:  $p > 0.05$  only for comparison with  $t = 170$  min. For



**Fig. 4:** Change with time of the mean fraction of cockroaches under the winning (square) and the losing shelter (triangle) for experiments with populations of (a) 10 cockroaches (14 replicates), (b) 16 cockroaches (19 replicates) and (c) 30 cockroaches (25 replicates).

16 cockroaches:  $F_{18,324} = 59.0$ ,  $p < 0.0001$ ; simple contrast test:  $p > 0.05$  only for comparison with  $t = 170$  min.). In the case of the populations containing 30 individuals, the mean number of cockroaches resting under shelters reached a plateau value between the 130th and the 180th minute (Fig. 4c. One-way repeated measures ANOVA on arcsine-transformed proportions:  $F_{18,306} = 67.9$ ,  $p < 0.0001$ . Simple contrast test:  $p > 0.05$  only for comparison with time  $\geq 130$  min.).

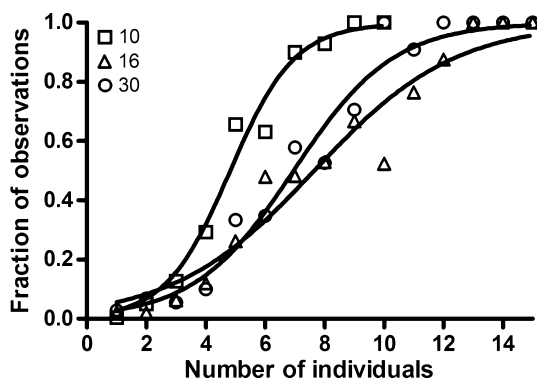
#### Relation Between Cluster Size and Shelter Selection

We found that a cockroach population is able to select one shelter as a common resting site. The disagreement between theoretical and experimental distributions (Fig. 2) has demonstrated that local

interactions between individuals are essential in this collective decision-making process. To determine the critical number of individuals required to select a shelter, we analysed the relationship between the probability of a shelter of becoming « selected » and the number of sheltered individuals during the course of an experiment.

At each time step  $i$  ( $i = 0, \dots, f$ ), the winning shelter of the  $m$ th replicate contains  $W_{mi}$  individuals and the loser  $L_{mi}$ .  $E(X)$  is the number of observations where  $W_{mi}$  is equal to  $X$  and from this time step  $W_{mk}$  remains always  $\geq L_{mk}$  ( $k = i, \dots, f$ ) until the end of the experiment ( $k = f$ ).  $Q(X)$  is the number of observations where  $W_{mi} = X$ . Our probability of exhibiting an irreversible choice  $P(X)$  when the value  $X$  is reached is the ratio between  $E(X)$  and  $Q(X)$ .

For the three population sizes, the sigmoid shape (logistic function) of  $P(X)$  shows that the selection process is based on the existence of a threshold value in the cluster size (Fig. 5. Goodness of fit test. For 10 cockroaches,  $R^2 = 0.98$ ,  $p = 0.88$ ,  $df = 6$ ; for 16 cockroaches,  $R^2 = 0.95$ ,  $p = 0.43$ ,  $df = 12$ ; for 30 cockroaches,  $R^2 = 0.97$ ,  $p = 0.06$ ,  $df = 23$ ). Moreover, the population size influences the aggregation patterns, as the curve for 10 individuals qualitatively differs from the ones obtained for 16 and 30 cockroaches. Indeed, for populations of 10 cockroaches, the increase of the curve is steep, with a threshold number of five cockroaches above which more than 50% of observations lead to the final selection of this shelter. On the other hand, this threshold number grows to seven individuals for populations of more than 10 cockroaches.



**Fig. 5:** Relation between the number of individuals under a shelter and the proportion of experiments leading to the selection of this shelter [ $P(X)$ ] for populations composed by 10 (square), 16 (triangle) or 30 (circle) cockroaches.

## Discussion

Our experiments show that the spatiotemporal distribution of cockroaches among shelters is not random. Indeed, when presented the choice between two identical shelters, individuals do not settle down equally between both sites as predicted by the ideal free distribution theory (Fretwell & Lucas 1970). Instead, we confirmed previous results showing that the whole group is able to collectively select one out of two identical sites. It has been suggested that this collective selection results from an amplification processes based on the decrease of the individual probability to leave the shelter with the presence of congeners under this shelter (Amé et al. 2006a; Halloy et al. 2007). Despite agreements between theoretical and experimental results, these previous studies suffer from some of the following gaps. Indeed, the aggregation dynamics was not recorded, and therefore the validation of the model was only based on the comparison between the theoretical and experimental stationary regimes (after 24 h). Our observation of short-term dynamics (during the first hours) highlights some phenomena not predicted by the model and/or not previously experimentally shown, notably concerning the speed of collective shelter selection and the existence of a quorum. In these previous studies, the influence of the size of the cockroach population was not tested at all (Amé et al. 2004) or only through the influence of the relative density corresponding to the ratio between the population size and the carrying capacity of the shelter (Amé et al. 2006a). Lastly, concerning isolated individuals, contrary to previous study, their behaviour was tested within the same setup as the other population size.

The present study confirms that the high density of cockroaches observed in these resting sites is partly because of the shelters darkness and to a mechanism of shelter selection based on an amplification process (Jeanson & Deneubourg 2007). By using a simplified experimental setup, we have limited the cues that cockroaches can perceive and that may act upon their decision. First, since cockroaches have neither explicit knowledge about the setup design (e.g. location of shelters) nor about the global spatial distribution of congeners (e.g. the size, number and location of aggregates), the decision of individuals to stay under a shelter relies on individual preferences as well as on the perception of two local cues: (1) the darkness under shelters and (2) the interactions with congeners. Indeed, an encounter with a shadowed area influences the cockroaches'

decisions: individuals rest longer and are more likely to stop walking in this area (Meyer et al. 1981). Such a preference for darkened areas explains why cockroaches tend to aggregate under shelters but cannot explain why the majority of cockroaches selects only one of the two available shelters. To account for shelter selection, we have to consider a factor modulating the resting time of cockroaches and acting as a positive feedback based on the number of conspecifics already present under the shelter.

We found out that the fraction of sheltered individuals is density-dependent and tends to increase with the size of the cockroach group, especially when we compare the response of isolated or few (10 and 16) individuals with larger cockroaches populations (30 cockroaches). This experimental demonstration is in agreement with classical theory on amplification mechanisms. If globally the final aggregation pattern (shelter selection) seems to be relatively comparable for the tested group sizes (10, 16 and 30 cockroaches), the spatiotemporal dynamics leading to their formation differs. Interestingly, the increase of the cockroach density speeds up the selection of one shelter for the majority of experiments. Furthermore, depending on the observation time and on the group size, the number of individuals under one of the shelters can show a transient monomodal distribution (equal number of cockroaches under each shelter). The observation of such different distributions in the same experimental conditions is a hallmark of a nonlinear phenomenon. For group of 30 cockroaches, the majority of experiments end with a large number of sheltered individuals and with the selection of one of the shelters, while no selection was observed in other experiments. Despite that the carrying capacity of each shelter is larger enough to contain the whole population size, cockroaches are distributed equally under both shelters in those few cases: this is because of cockroaches (of which the number is sufficient) initiating an aggregation in each of the two shelters and maintaining it for the entire duration of the experiment. This state predicted theoretically was never observed before. However, following theoretical predictions (Amé et al. 2006a), it is an unstable state that should lead, after a while, to the gathering of all individuals under the same shelter (e.g. after 24 h).

Moreover, our results show that a quorum of individuals resting under a shelter has to be reached to ultimately lead to the selection of one shelter. This quorum consists in a sufficiently larger number of sheltered individuals than cockroaches entering into

it will tend to stay and swell the ranks of the aggregate. Moreover, we demonstrate the stability and the irreversibility of the selection because of the amplification processes when the quorum is reached. For small groups of 10 cockroaches, the selection of one shelter takes a relatively long time to be initiated (more than 100 min, Fig. 2) because of the difficulty of reaching the quorum of individuals required to attract and maintain conspecifics under the same shelter. Indeed, in more than 50% of experiments, no definitive choice between shelters had been made even after 180 min. Such a delay in the collective selection of an aggregation site should be linked to the low probability of getting individuals entering shelters and as a consequence, to get two or more cockroaches concomitantly resting under the same shelter. For larger populations, the quorum is reached more quickly, what results into a higher rate of selection, even though the transient occupation of both shelters may be observed in some experiments.

The existence of a quorum that triggers a change in behaviour and/or in physiology has been found in many different species and in several contexts. A well-known example is the density-dependent phase polyphenism of locusts. Here, crowding stimulates individuals to change from the shy, cryptically coloured, solitary phase into the conspicuously coloured, swarm-forming, gregarious phase (Collett et al. 1998; Simpson et al. 1999). Likewise, the soldier production in social aphid species is elicited by mechanosensory inputs when – at high population densities – the rate of direct contacts exceeds a certain threshold value (Shibao et al. 2004). In addition, during the new nest site selection by the ant *Temnothorax albipennis* for example, individuals switch from tandem runs to transports according to the density on the new site (Pratt et al. 2002; Pratt 2005, 2008). In bees, quorum in the new nest site is also a key-element in the formation and the takeoff of the swarm (Seeley & Visscher 2004). This mechanism allows the coordination of individuals in the performance of certain behaviour with their local density as the only cue (Diggie et al. 2007). In the present study, the time spent to reach this quorum and then to start the aggregation process of cockroaches depends on the total population size.

To conclude, this aggregation behaviour of cockroaches is characterized by bifurcation patterns, including transient state with an equal number of cockroaches under each shelter and a quorum process. If previous models predict the steady-state at the end of the aggregation process (Amé et al. 2006a), their dynamics were poorly studied and for

example, it was not shown that they exhibit a quorum. These models should be improved by confronting their future analysis to our results.

In the absence of a global knowledge of the environment, cockroaches are nevertheless able to assess the availability of resources and to aggregate in the same resting site. This laboratory observation is confirmed by studies on the field showing that the aggregate is a limited area composed of contiguous dark places like cracks in the walls, pipes and corners (Rivault 1989). This area occupies the central part of a foraging area and cockroaches keep returning to the same shelter after exploratory trips (Rivault 1990). Future research should also study how the shelter quality, their number or their spatial distribution interplay with individual preferences and influence the population dynamics and the collective decision of cockroaches in a patchy environment.

In cockroaches, the influence of congeners and the modulation of the resting time are based on the discrimination and the recognition of cuticular hydrocarbon profiles through antennal contacts of congeners cuticle. Cockroaches prefer to aggregate with individuals having similar cuticular signature (strain members recognition: Rivault et al. 1998; kin recognition: Lihoreau & Rivault 2009), but they also aggregate with other cockroaches species (Leoncini & Rivault 2005; Saïd et al. 2005). Moreover, it was demonstrated for *P. americana* that the perception of these chemical compounds on an object increases the mean resting time of cockroaches around it (Sempo et al. 2006c). The importance of these cuticular hydrocarbons in the aggregation process was notably demonstrated through the formation of mixed aggregates composed by cockroaches and robots, the latter displaying notably the same external chemical profile (Sempo et al. 2006c). It was notably demonstrated that similar phenomenon modulating the resting time of individuals is independent of the nature of the interaction and points to a generic self-organized collective decision-making process independent of animal species. Similar positive feedbacks have already been experimentally observed in several insects and vertebrates (Rivault et al. 1998; Camazine et al. 2001; Detrain & Deneubourg 2006; Depickère et al. 2004; Amé et al. 2004; Jeanson et al. 2005; Jeanson et al. 2004; Couzin et al. 2005; Sumpter 2006; Dussutour et al. 2007). We would expect that the collective decision-making process highlighted for cockroaches, which notably includes a quorum decision-making process, is somehow generic and that any group-living species sharing the same structure of interactions and similar

spatiotemporal patterns should present the same type of collective decision capabilities regardless of its level of social complexity (Lefebvre 1985; Danchin et al. 2004; Costa 2006).

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