

Self-Organized Aggregation Triggers Collective Decision Making in a Group of Cockroach-Like Robots

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Self-amplification processes are at the origin of several collective decision phenomena in insect societies. Understanding these processes requires linking individual behavioral rules of insects to a choice dynamics at the colony level. In a homogeneous environment, the German cockroach *Blattella germanica* displays self-amplified aggregation behavior. In a heterogeneous environment where several shelters are present, groups of cockroaches collectively select one of them. In this article, we demonstrate that the restriction of the self-amplified aggregation behavior to distinct zones in the environment can explain the emergence of a collective decision at the level of the group. This hypothesis is tested with robotics experiments and dedicated computer simulations. We show that the collective decision is influenced by the available spaces to explore and to aggregate in, by the size of the population involved in the aggregation process and by the probability of encounter zones while the robots explore the environment. We finally discuss these results from both a biological and a robotics point of view.

Keywords self-organization · aggregation · collective decision · *Blattella germanica* · swarm robotics

1 Introduction

Decision-making mechanisms are of crucial importance for any animal. They allow it to behave differently according to its needs and according to the environmental situation: the decision results from the integration over time of what the animal perceives and what its aims are. The elucidation of such mechanisms is therefore central to understanding how an animal deals with heterogeneous environments.

If decision-making mechanisms are essential for a single individual, they are also crucial for the organi-

zation of animal groups. In particular collective decision making (i.e., the ability for the group's members to reach a consensus on a common action to carry out) is a cornerstone for the organization of animal societies (Camazine et al., 2001; Conradt & Roper, 2005; Couzin, Krause, Franks, & Levin, 2005; Garnier, Gautrais, & Theraulaz, 2007). It is involved at different stages of the group's life, from the choice of a place to live to the selection of a profitable food source or of a direction to follow.

In order to reach a consensus the group members may refer to one or a few leaders that decide for the

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whole community. Such behavior can be observed in certain animal groups where few individuals guide the activities of the others. In social insects, however, collective decision making relies on a different principle. Their collective choices are often based on self-organization processes (Camazine et al., 2001; Couzin et al., 2005; Garnier et al., 2007; Sumpter, 2006), as for instance in target selection in bees (Millor, Pham-Delegue, Deneubourg, & Camazine, 1999) or in food source selection (Beckers, Deneubourg, Goss, & Pasteels, 1990) and path selection (Beckers, Deneubourg, & Goss, 1992) in ants. In each of these cases, some insects discover independently different opportunities in the environment and recruit other nest mates toward these opportunities. The recruited nest mates can, in turn, recruit other nest mates, and so on. This is a self-amplification process: the more individuals that signal an opportunity, the more likely other individuals will join them. Because the number of individuals that can be recruited is limited (e.g., because of the size of the colony), a competition arises between the different opportunities to attract the greatest number of individuals. Eventually, the winning opportunity is the one with a faster self-amplification process than the other. The decision is not taken by one or a few individuals in the group but rather emerges from the numerous interactions among the members of the group.

Such self-organization processes present several interesting features for the achievement of multi-robot tasks: the individual behaviors are often simple compared with the complex colony output; the colony is flexible to changing environmental conditions; the redundancy makes the colony tolerant to individual failures (Bonabeau, Dorigo, & Theraulaz, 1999; Sahin, 2005). This has encouraged the development of *swarm robotics*, a branch of collective robotics, which has made an explicit use of bio-inspired self-organization to coordinate groups of robots in various contexts: dispersion (McLurkin & Smith, 2007), aggregation (Beckers, Holland, & Deneubourg, 1994; Garnier et al., 2008), segregation/sorting (Wilson, Melhuish, Sendova-Franks, & Scholes, 2004), coordinated movement (Baldassarre et al., 2007), coverage (Correll, Rutishauser, & Martinoli, 2008), target localization (Hayes & Dormiani-Tabatabaei, 2002), task allocation (Labella, Dorigo, & Deneubourg, 2006), cooperative manipulation (Kube & Bonabeau, 2000; Martinoli, Easton, & Agassounon, 2004) and foraging (Krieger, Billeter, & Keller, 2000).

Because swarm robotics is mainly a bio-inspired discipline dealing with artificial systems, its results can be interpreted from different points of view. From an engineer's point of view it displays alternative mechanisms to organize the activities of groups of autonomous robots. From a biologist's point of view it is an interesting tool to formulate and test hypotheses about the organization of animal societies. In this article our goal is to investigate a self-organized decision-making process from both points of view based on a collective robotics implementation. On the one hand we want to test whether the self-organized aggregation behavior of the German cockroach *Blattella germanica* may account for its ability to select places in heterogeneous environments. On the other hand we want to show that this self-organized process may be used as a place-selection mechanism for groups of autonomous mini-robots.

In recent works, Jeanson et al. (2003, 2005) have demonstrated that the aggregation behavior displayed by the German cockroach *B. germanica* relies on a self-organization process: for a given moving cockroach, the larger the number of staying neighbors, the more likely the animal is to stop and stay beside them. This leads the cockroaches to quickly aggregate in dense clusters in a homogeneous environment. The natural habitat of *B. germanica* is, however, heterogeneous: some places are more attractive for cockroaches, thus promoting aggregation in particular sites. For instance, cockroaches preferentially aggregate in dark places (Rust, Owens, & Reiersen, 1995). If one puts a dark shelter in a bright arena, one will observe that cockroaches strongly aggregate under this shelter. If two or more dark shelters are placed in the arena, a majority of the cockroaches will aggregate under a single shelter rather than evenly spreading among all resting sites (Ledoux 1945). The group therefore selects a place to aggregate among several available in its environment.

In this article, we investigate the behavioral mechanism at the origin of this collective choice. In a recent article, Ame, Halloy, Rivault, Detrain, and Deneubourg (2006) suggested that this collective choice can be explained by a modulation of the individual staying time under a dark shelter by the number of nest mates already present under this shelter: the more cockroaches there are, the longer time a cockroach will stay under this shelter. Their mean-field model assumes, however, that this modulation of the individual's

behavior is linked to the overall density of cockroaches under the shelter. Therefore, cockroaches should have a global perception of the number of conspecifics under the shelter they occupy. Here, we propose rather that this modulation is achieved only by the local perception of the proximate neighbors. In particular, we propose that it is a consequence of the self-organization process studied by Jeanson et al. (2005) that triggers aggregation in cockroaches when they are placed in an homogeneous arena. We hypothesize that, if the occurrence of aggregation behavior is restricted to or favored in several spatially distinct areas between which cockroaches can move, competition should arise between the potential aggregation sites which should end with the collective selection of only one of them.

To investigate this hypothesis, we use an approach mixing both robotics experiments and computer simulations. On the one hand the robotics implementation allows the testing of the behavioral model in practice and in context, that is, in terms of real problems in real environments. It is the proof-of-concept that the aggregation behavior can be used as a place-selection mechanism for groups of autonomous robots. It is also a validation of our biological hypothesis that the aggregation behavior of *B. germanica* actually drives its place-selection behavior (for a review of the robotics approach to animal behavior see: Dean, 1998; Webb, 2000, 2001). Note that this robotics approach has been successfully employed to study individual animal behaviors related to motor or sensorimotor control (e.g., Franceschini, Pichon, & Blanes, 1992; Pfeiffer, Eltze, & Weidemann, 1995), navigation (e.g., Lambrinos, Moller, Labhart, Pfeifer, & Wehner, 2000; Srinivasan et al., 1999) or learning (e.g., Voegtlin & Verschure, 1999). In a collective behavior context, it has been applied to study aggregation (Garnier et al., 2008; May et al., 2006), stigmergic processes (Beckers et al., 1994; Holland & Melhuish, 1999; Melhuish, Wilson, & Sendova-Franks, 2001), cooperative transport (Kube & Bonabeau, 2000), the influence of task allocation and group size on foraging efficiency (Krieger & Billeter, 2000; Krieger et al., 2000) and the influence on collective place selection of robotic lures in animal groups (Halloy et al., 2007).

On the other hand the computer simulations approach aims at exploring more systematically the properties of the behavioral model. The simulations allow the investigation of the collective selection

mechanism in an extended set of environmental conditions. They thus bring additional information about the collective behavior of the robotics system. Seen from a biological point of view this information may also open interesting insights about the collective behavior of our biological model. To ensure the coherence between the virtual implementation and the physical embodiment of the behavioral model, the computer simulations are calibrated to the robotics experiments.

With this dual approach, we first test whether the self-amplified aggregation behavior of the German cockroach is capable of triggering a collective choice between two identical opportunities. In a recent work, we have implemented this aggregation behavior in a group of small autonomous robots, and we have successfully reproduced the aggregation dynamics displayed by *B. germanica* in a homogeneous circular arena (Garnier et al., 2008). Here, we introduce heterogeneities into the circular arena in the form of two identical dark shelters. Contrary to the aggregation experiments in Garnier et al. (2008) where robots could move and stop everywhere in the experimental arena, here we restrict the occurrence of the aggregation behavior to the dark shelters: robots can move everywhere in the arena, but are programmed not to stop outside the shelters. While under a shelter, they continue their displacement unless they decide to stop with a probability that increases according to the number of proximate neighbors they perceive, as in Garnier et al. (2008). If stopped under a shelter, their probability of restarting decreases with the number of proximate neighbors they perceive, still as in Garnier et al. (2008). If our hypothesis that the aggregation behavior of cockroaches supports their collective selection ability is correct, the robots should aggregate under a single shelter.

We further investigate with computer simulations whether this choice between equal opportunities is sensitive to the available space for aggregation. Keeping the number of virtual robots constant, we vary the radius of the shelters, from shelters too small to house the whole group of robots to shelters much bigger than required to house all the robots. We repeat these virtual experiments with different numbers of robots in order to evaluate how the response scales with the group size.

In a second step we test how the collective decision mechanism deals with physically different oppor-

tunities. Collective choices are known to be sensitive to the physical differences between opportunities that are in competition. In particular, any constraint that modulates the speed of the self-amplification process at one of the different opportunities can lead that opportunity to win, or lose, its competition against the other ones (Camazine et al., 2001; Jost et al., 2007). In this article, we assess the influence of a difference between the radii of the two shelters on the final choice. To that purpose, we run two sets of robotics experiments, each time with one shelter bigger than the other one. In the first set of experiments, the smaller shelter can hardly house the whole group of robots while the bigger one can do so. In the second set of experiments, both shelters are large enough to house the whole group of robots. These two situations differ from each other only by the influence of the physical obstruction to enter the smaller shelter. When some other robots are already there the new arrivals are less likely to enter the smaller shelter in the first situation only. We therefore expect that the group behaves differently between these two nearly identical situations.

In order to study in more detail the influence of the ratio between the sizes of the two shelters on the final choice, we use computer simulations where we confront a group of 10 virtual robots with one shelter of constant size and one shelter in which size varies between simulation runs.

We finally discuss the results of both robotics experiments and computer simulations from our dual point of view. We examine in particular how the collective decision model tested in this article may account for various observations of cockroach collective behavior in both experimental and natural contexts. We also consider the interest for collective robotics of the properties displayed by this embodied model.

2 Material and Methods

2.1 Alice Micro-Robots

The Alice micro-robots (see Figure 1) were designed at the EPFL (Lausanne, Switzerland; Caprari & Siegwart, 2005). They are very small robots (22 mm × 21 mm × 20 mm) with a maximum speed of 40 mm s⁻¹. They are equipped with two watch motors with wheels and tires. Four infrared sensors and transmitters are used for obstacle detection and local commu-



Figure 1 An Alice robot heading toward the left side.

nication among Alices. Energy is provided by a NiMH rechargeable battery allowing an autonomy of about 6 h in the configuration used during this study. The Alice robots have a micro-controller PIC16LF877 with 8K Flash EPROM memory, 368 bytes RAM and no built-in float operations. Programming is done with the IDE of the CCS-C compiler and the compiled programs are downloaded in the Alice memory with the PIC-downloader software¹.

2.2 Experimental Setup

The experimental setup consists of a circular arena (25 cm radius) covered with a glass plate and two freely suspended semi-transparent dark discs that act as shelters. A 60-watt glow light is suspended 60 cm above the arena to generate a background infrared light of homogeneous intensity (the robots only detect infrared light). All other light sources are eliminated. This experimental setup aims at reproducing the one used by Amé et al. (2006). Three shelter sizes are used: small (radius $r_{small} = 5$ cm), medium (radius $r_{medium} = 7$ cm) and large (radius $r_{large} = 9$ cm). In theory, these three kinds of shelters are all sufficiently large to house the whole population of robots: the minimal known radius of the circle required to house 10 packed squares measuring 2.1 cm on each size is $r_{10} = 4.45$ cm (Friedman, 2007). However, the 10 robots cannot aggregate under the small shelter if they do not adopt a particular configuration. In practice, physical obstruction prevents the whole group from aggregat-

ing under the small shelter. Experiments were conducted with groups of 10 robots and they lasted 60 min each. In order to record robot behaviors, a high definition camera (Sony CDR-VX 2000 E) was attached above the arena.

2.3 Behavioral Model

The behavioral model we use in this work is an extension of the aggregation model described by Jeanson et al. (2003, 2005) and implemented in robots by Garnier et al. (2008). The original behavioral model was developed from experiments with first instar larvae of the German cockroach, *Blattella germanica*. In its natural environment, *B. germanica* forms dense aggregates of individuals of both sexes and at all developmental stages especially at low external humidity (Dambach & Goehlen, 1999; Ledoux, 1945). The original behavioral model accounted for the self-organized mechanism that led to aggregation behavior.

The complete aggregation model and its implementation are described by Garnier et al. (2008) and outlined in the Appendix. In summary, each robot explores the experimental arena by a correlated random walk in the absence of obstacles or by a wall-following behavior in the presence of large obstacles. Each robot can stop its displacement at any time. The decision to stop is taken according to a memory-less process: it is independent of the previous experience of the robot, therefore the probability of stopping per unit time (stop rate) is constant in time. However, it depends on the number of stopped robots that a robot perceives in its direct neighborhood (up to ≈ 4 cm distance). The stop rate of a robot grows with this number and it reaches a maximum when three or more neighbors are detected.

Once stopped, the robot decides whether the stop is of short or long mean duration. The probability of a short duration stop decreases with the number of neighbors, with a minimum when three or more neighbors are detected. The decision to restart is also a memory-less process. The probability of restarting per unit time is therefore constant in time. However, it depends on the state of the stop (short or long) and on the number of neighbors. It is maximal for a short stop with no neighbors, and minimal for a long stop with three or more detected neighbors.

In the extended model used in this article, this aggregation behavior is restricted to dark places in the

environment. A robot can only stop if it perceives a significant drop in the background infrared light intensity that it detects with its infrared sensors. This drop informs the robot that it enters a shelter. This rule restricts the aggregation behavior to the dark places and is the only addition to the original aggregation model from Jeanson et al. (2005) and Garnier et al. (2008).

2.4 Experimental Parameters

2.4.1 Identical Shelters In the first set of 20 experiments, the robots were put into an arena with two shelters of the same size (medium size, radius $r_{medium} = 7$ cm). The goal of this situation was to demonstrate the ability of the behavioral model to trigger a collective choice, even if the two offered opportunities are equivalent. At the beginning of each experiment, 10 robots were evenly distributed within the arena. We then suspended two medium shelters and let the robots aggregate for 60 min.

2.4.2 Shelters of Different Sizes In this second set of experiments, the robots were put into an arena with two shelters of different radius. The goal of these experiments was to study whether a difference between the two opportunities would bias collective choice. Two situations were tested: a shelter of small size (radius $r_{small} = 5$ cm) versus a shelter of medium size (radius $r_{medium} = 7$ cm), and a shelter of medium size versus a shelter of large size (radius $r_{large} = 9$ cm). For each situation, 20 experiments were performed. At the beginning of each experiment, 10 robots were evenly distributed in the arena and we let them aggregate for 60 min.

2.5 Numerical Experiments

In addition to the robotic experiments, we ran several sets of spatially explicit individual-based simulations to further explore the model properties. The simulator takes into account the spatial obstruction between the individuals in order to reproduce the physical exclusion of the robots under crowded shelters. For the purpose of computing efficiency, the spatial obstruction is not obtained using a physics engine but rather by mimicking the avoidance behavior of the robot observed in experiments after a collision with another robot (they move slightly backward and wobble). This

simulator has already been validated for aggregation behavior by Garnier et al. (2008). We also validated the simulator against experimental results for collective choice behavior to ensure coherence between robotics and virtual experiments.

With these simulations we addressed two specific questions. First, how does collective choice scale with group size and with changing available space for aggregation (i.e., the space covered by the two shelters)? To answer this question we varied the radius of the two shelters simultaneously from 0 to 5 times (in steps of 0.1) the minimal known radius r_n of the circle required to house n packed squares, with $n = 5, 10, 20, 50$ robots and $r_5 = 3.32$ cm, $r_{10} = 4.45$ cm, $r_{20} = 6.08$ cm, and $r_{50} = 9.26$ cm (Friedman, 2007). The radius of the arena was chosen such that the ratio between the surface of the arena and the cumulated surface of the shelters remained constant. This ensured that a robot at the start of the experiment had the same probability to start under a shelter or in the rest of the arena. We ran 1,000 replications by size step and each simulation corresponded to 60 min in real time.

Second, how do differences between the sizes of the two shelters bias collective choice? To answer this question we fixed the radius of one shelter (7 cm, medium size shelter) while we varied the radius of the other one from 1 cm to 50 cm (i.e., from 0.14 to 7.14 times the radius of the constant shelter) by steps of 1 cm. The idea was to extend the range of radius values tested in the experimental part of the work. In particular, we observed how the ratio between the radius of the two shelters influenced the final choice of the group. For ratio values away from 1 (either superior or inferior), we expected a qualitative change of the collective choice, with group of robots selecting almost systematically one particular shelter rather than the other. The size of the arena was varied to fix the ratio between the surface of the arena and the cumulated surface of the shelters. This ensured that a robot at the start of the experiment had the same probability to start under a shelter or in the rest of the arena. We ran 1,000 replications by radius size and each simulation corresponded to 60 min. This sensitivity analysis was performed for a group of 10 robots.

2.6 Data Analysis

All analyses were done with the open source statistical software R (R Development Core Team, 2006).

2.6.1 Experiments For each experiment, we counted at each minute the number of stopped robots under each shelter. For convenience, we call the shelters S_1 and S_2 . For each experiment, we thus obtain m_{s_1} (the number of robots stopped under shelter S_1), m_{s_2} (the number of robots stopped under shelter S_2) and m_{tot} (the total number of robots). In the robotics experiments, we have $m_{tot} = 10$.

For the experiments with identical shelters, we defined in each replication the chosen shelter as the one that contained the largest number of stopped robots at the end of the experiment. We then computed the mean number of robots under the chosen and the not-chosen shelters minute by minute. We also computed the fraction of the stopped robots which are under shelter S_1 at the end of each experi-

ment as $F_{Stop, S_1} = \frac{m_{s_1}}{m_{s_1} + m_{s_2}}$. From this last statistic we derived what we call a “choice distribution” which corresponds to the distribution of the F_{Stop, S_1} over all the replications.

Note that a robot can be in three different locations at the end of an experiment: under one of the two shelters or outside the shelters. In the case of each robot randomly choosing a shelter (i.e., without any influence of its conspecifics), the result follows a trinomial law with parameters $m_{tot} = 10$ (number of

robots), $p_a = \frac{(m_{tot} - m_{s_1} - m_{s_2})}{m_{tot}}$ (probability for a robot to be outside the shelters, estimated from the experi-

ments), $p_{s_1} = (1 - p_a) \left(\frac{r_{s_1}^2}{r_{s_1}^2 + r_{s_2}^2} \right)$ (probability for a robot to be under shelter S_1 ; r_{s_1} , radius of shelter S_1 ; r_{s_2} , radius of shelter S_2) and $p_{s_2} = 1 - p_{s_1} - p_a$ (probability for a robot to be under shelter S_2). The choice distribution resulting from this trinomial law is obtained through Monte Carlo simulations (10,000 simulations of 20 replications). We compared this random choice distribution with the experimental choice distribution by means of a chi-square test.

For the experiments with different shelters, we always considered the medium shelter as shelter S_1 and either the small or the large shelter as shelter S_2 . For every minute, we computed the mean number of robots under shelters S_1 and S_2 . We also computed the choice distribution in the two different situations. The resulting choice distributions were compared with the

corresponding trinomial distributions by a chi-square test and with the choice distribution of the identical shelters case by a Fisher's exact test.

To ensure the correspondence between the robotics and the virtual experiments, three sets of simulations corresponding to the three experimental situations described in Section 2.4 were analyzed with the same methods as those described above. Additionally, the choice distributions for these three sets of simulations were compared with the corresponding experimental choice distribution using Fisher's exact test.

2.6.2 Sensitivity Analysis The goal of the sensitivity analysis was to assess how the collective choice depends on either the sizes of the two shelters (identical shelters case) or the ratio between the two shelter sizes (different shelters case). We therefore defined the control parameter for the sensitivity analysis in the identical shelters case as the ratio $\frac{r_s}{r_n}$, with r_s the radius of the two shelters and r_n the size of the minimal known radius of the circle required to house n packed squares measuring 2.1 cm on each side (with $n = 5, 10, 20, 50$). In the different shelters case, we defined the control parameter as the ratio $\frac{r_{s_2}}{r_{s_1}}$, with r_{s_2} the radius of the shelter whose size varies (S_2) and r_{s_1} the radius of the shelter whose size remains constant and corresponds to a medium shelter (S_1).

To measure the variation of the collective choice, we computed for each replication the fraction of robots stopped under shelters S_1 and S_2 at the end of each experiment as $F_{S_1} = \frac{m_{S_1}}{m_{tot}}$ and $F_{S_2} = \frac{m_{S_2}}{m_{tot}}$. These fractions are slightly smaller than the fraction F_{Stop, S_1} of stopped robots which are under shelter S_1 since we also took into account the number of robots that remained moving at the end of the replication. In the experimental part, this number could be neglected (most of the robots are stopped under a shelter at the end of each experiment) and thus F_{Stop, S_1} was used. However, the number of robots still moving at the end of the replication cannot be neglected in the sensitivity analysis since the available space for aggregation should influence the total number of stopped robots. Indeed, when shelters are very large for instance, the probability for a robot of encountering an aggregate decreases, and hence its probability to stop, and the

number of moving robots can remain sizable at the end of a trial.

In the identical shelters case, we also computed the fraction $F_{S \geq 0.8}$ of replications that ended with either $F_{S_1} \geq 0.8$ or $F_{S_2} \geq 0.8$: this corresponded to the fraction of experiments that ended with at least 80% of the robots under one of the two shelters. In the different shelters case, we computed in the same manner the fraction $F_{S_1 \geq 0.8}$ of replications that ended with $F_{S_1} \geq 0.8$, the fraction $F_{S_2 \geq 0.8}$ of replications that end with $F_{S_2} \geq 0.8$ and the fraction $F_{S \geq 0.8} = F_{S_1 \geq 0.8} + F_{S_2 \geq 0.8}$ of replications that ended with either $F_{S_1} \geq 0.8$ or $F_{S_2} \geq 0.8$.

3 Results

3.1 Identical Shelters

3.1.1 Robotic Experiments Figure 2 displays typical spatio-temporal dynamics of the collective choice of a single shelter in both robotics and simulated experiments with identical shelters.

Figure 3a and c summarize the experimental results for the case with two identical shelters ($\frac{r_s}{r_{10}} = 1.57$). Figure 3a illustrates the temporal dynamics of the aggregated robots under the chosen and the unchosen shelters. These dynamics displayed two distinct phases. The first phase lasted approximately 10 min and displayed linear growth in the number of aggregated robots under the chosen shelter. At the end of this first period, about 50% of the overall population of robots was aggregated under the chosen shelter, while less than 10% was aggregated under the uncho-

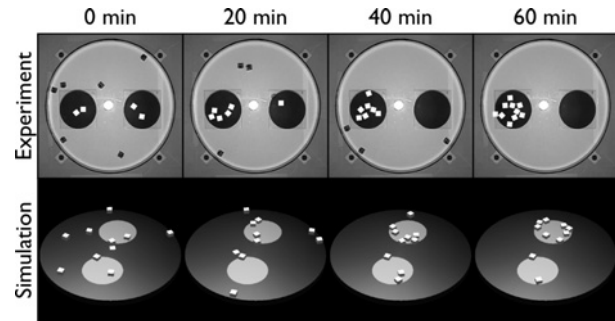


Figure 2 Typical temporal evolution of the collective decision process in a robotics experiment (top row) and a simulation run (bottom row). Robots under the dark shelters (top row) are visualized by white squares.

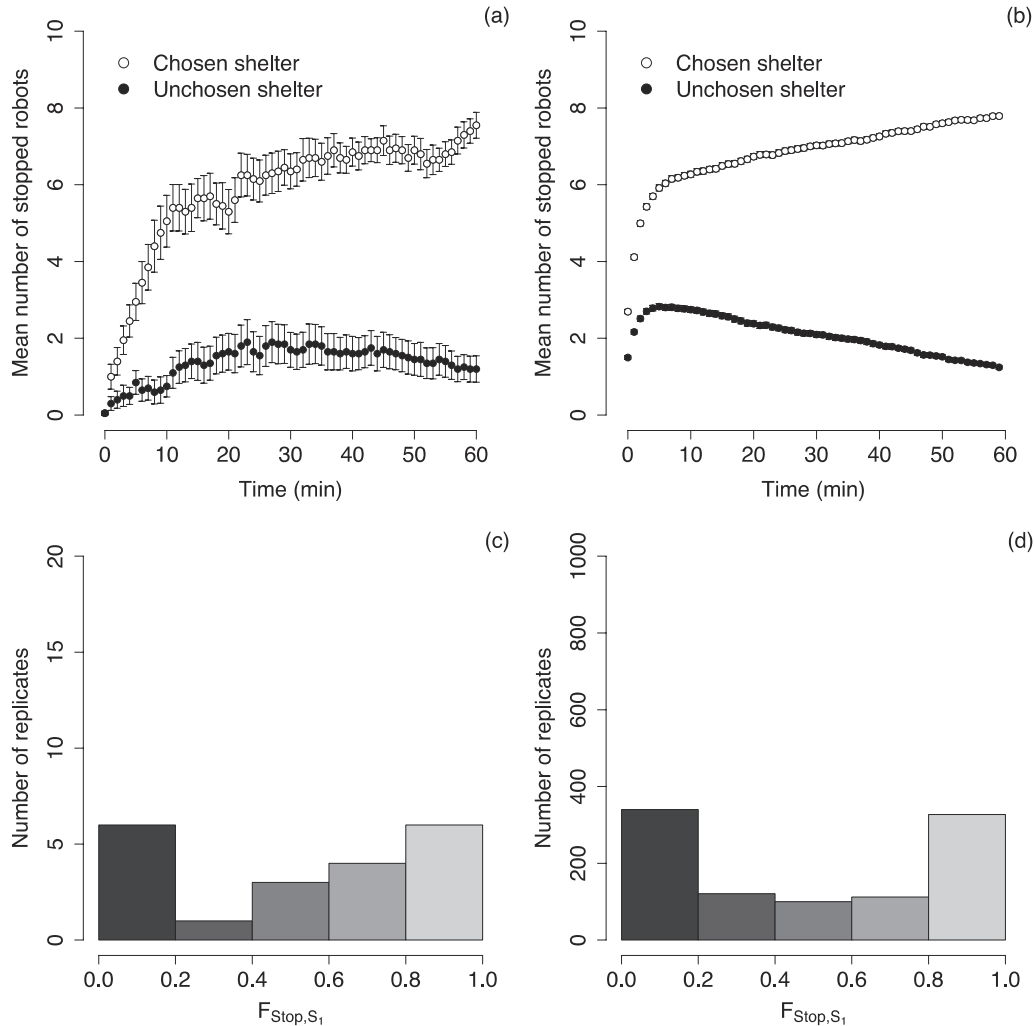


Figure 3 Results of the robotics experiments and the simulations with two identical shelters. **Top:** number of robots aggregated under each shelter per minute. (a) Experimental data ($n = 20$). (b) Simulation data ($n = 1000$). White dots represent data for the chosen shelter (i.e., the shelter which is chosen at the end of each experiment); black dots represent data for the unchosen shelter. Each dot represents the mean \pm SE (note that in the simulations the SEs were too small to be seen on the graph). **Bottom:** choice distributions. In these distributions, each block represents the number of experiments that ended with a given percentage (0–20, > 20–40, > 40–60, > 60–80, > 80–100%) of stopped robots under shelter 1 (independently of whether it was chosen or not). Extreme values of the distribution (between 0 and 0.2, and between 0.8 and 1) represent experiments that ended with at least 80% of the aggregated robots under shelter S_1 (0.8 to 1) or under shelter S_2 (0 to 0.2, i.e., experiments that ended with less than 20% of the robots under S_1). (c) Experimental distributions ($n = 20$). (d) Simulation distributions ($n = 1000$).

sen one. The second phase lasted until the end of the experiment. It also displayed a linear growth in the number of aggregated robots under the chosen shelter, but its slope was less marked than in the first phase. At the end of the experiments, $75.5 \pm 3.36\%$ (mean \pm SE) of the overall population was aggregated under the chosen shelter, while $12 \pm 3.44\%$ (mean \pm SE) was aggregated under the unchosen one.

Figure 3c illustrates the experimental choice distribution for shelter S_1 . This choice distribution was U shaped which is a typical signature of self-organized binary choices (e.g., see Amé et al., 2006; Beckers et al., 1992). Extreme values of the distribution (between 0 and 0.2, and between 0.8 and 1) represent experiments that ended with at least 80% of the aggregated robots under shelter S_1 (0.8 to 1) or under shelter S_2

(0 to 0.2, that is experiments that ended with less than 20% of the robots under S_1). Thus, the number of experiments that ended with more than 80% of the aggregated robots under a single shelter (either S_1 or S_2) is the sum of the number of experiments between 0 and 0.2 and between 0.8 and 1. Likewise, the number of experiments that ended with more than 60% of the aggregated robots under a single shelter (either S_1 or S_2) is the sum of the number of experiments between 0 and 0.4 and between 0.6 and 1.

Sixty percent of the experiments ended with more than 80% of the aggregated robots under a single shelter. Eighty-five percent of the experiments ended with more than 60% of the aggregated robots under a single shelter. The comparison of this experimental choice distribution with a random choice distribution was highly significant ($\chi^2 = 134.8$, $df = 1$, $p < .0001$, p -value simulated with 10,000 replications).

3.1.2 Simulator Validation Figure 3b and d summarize the simulation results for the case with two identical shelters. As for the robotics experiments (see Figure 3a), the choice dynamics displayed in the first minutes illustrated rapid linear growth in the number of aggregated robots under the chosen shelter, followed by a slower growth phase during the remaining time. At the end of the simulations, $77.9 \pm 0.52\%$ (mean $\pm SE$) of the overall population was aggregated under the chosen shelter ($68 \pm 3.2\%$ in the experiments), while $12.45 \pm 0.48\%$ (mean $\pm SE$) was aggregated under the unchosen one ($12 \pm 3.44\%$ in the experiments). Moreover, the comparison between the simulated (see Figure 3d) and the experimental (see Figure 3c) choice distributions was not significant (Fisher's exact test, $p = .5759$).

3.1.3 Sensitivity Analysis Figure 4 summarizes the sensitivity analysis for the identical shelters case. It represents the fraction of replications ending with at least 80% of the robots aggregated under the same shelter ($F_{S \geq 0.8}$) as a function of the ratio between the radius of the shelters and the minimal known radius of the circle required to house the whole group of robots ($\frac{r_s}{r_n}$). The curves for 5, 10, 20, and 50 simulated robots displayed a common pattern. Below a threshold ratio $\frac{r_s}{r_n}$, no replication ended with at least 80% of the

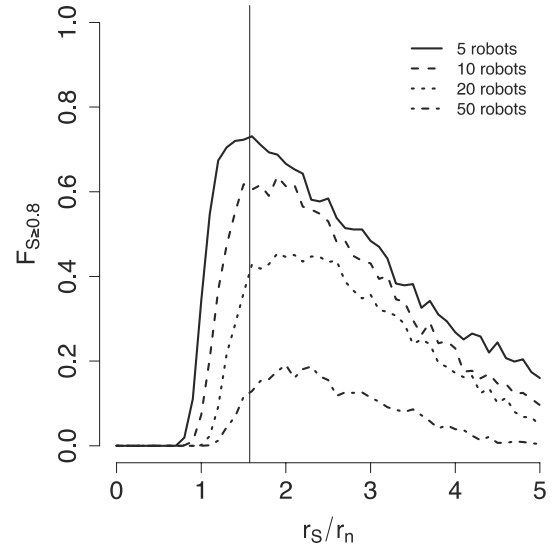


Figure 4 Identical shelters case. Fraction of simulation replications that ended with at least 80% of the robots aggregated under the same shelter ($F_{S \geq 0.8}$) as a function of the ratio between the radius of the two identical shelters (r_s) and the minimal known radius of the circle required to house the whole group of robots (r_n). One thousand simulation replications were performed for each value of $\frac{r_s}{r_n}$ and for each group size (5, 10, 20, and 50 robots). The vertical line corresponds to the ratio $\frac{r_s}{r_n}$ used in the experiments with 10 robots.

robots aggregated under the same shelter. This corresponded to ratio values for which r_s was too small to house 80% of the robots, therefore a trivial case.

After this initial part, $F_{S \geq 0.8}$ quickly grows with $\frac{r_s}{r_n}$ until reaching a plateau, and finally decreases as r_s becomes much larger than r_n . This final decrease was mainly the result of the increase of the available space as a consequence of the constant ratio between the surface of the arena and the cumulated surface of the shelters (see Section 2.5). As r_s grows the available space under each shelter and outside the shelters grows. This decreases the probability that a robot will encounter an aggregate and therefore reduces the probability of obtaining a large and stable cluster under one of the two shelters.

Despite this common pattern, the sensitivity analysis revealed a difference between the different group sizes. This difference was a decrease of the values of

$F_{S \geq 0.8}$ as the number of robots increased. For instance, the maximal value of $F_{S \geq 0.8}$ varied from 0.73 for 5 robots to 0.19 for 50 robots. At the plateau, this meant that more than 70% of the replications with 5 robots ended with at least 80% of the robots under one of the two shelters. This percentage of replications drops below 20% with 50 robots: few replications with 50 robots end with a clear choice for one of the two shelters. With 50 robots, it is likely that several large aggregates (10 robots or more) appear during the collective choice process. The time spent by a robot in an aggregate is maximal when this robot is surrounded by at least three neighbors. In a group of 10 or more robots, it is likely that several robots are surrounded by at least three neighbors. As a consequence, such aggregates were very stable. If one large aggregate formed under each shelter, it is therefore likely that the competition between them lasted a long time (more than the 60 min during the experiment) before one of them captured most of the robots and the collective decision occurred. Even after 120 min (data not shown), no choice was reached with a population of 50 robots. Two other observations support this idea. First, aggregates of the German cockroaches *B. germanica* rarely include more than 30 individuals (Rust et al., 1995). Second, a comprehensive analysis of the cockroach aggregation model showed that at stationary state the mean number of aggregates formed by 40 cockroaches is two (data not shown). Therefore, it is likely that large populations of robots and cockroaches are not able to reach a consensus and rather split between the different available shelters.

3.1.4 Summary of Identical Shelters Case In robotic experiments, when the group of robots faced two identical shelters, most of the experiments ended with a choice of either shelter S_1 or shelter S_2 . The German cockroach aggregation behavior is therefore able to trigger a collective choice, even if the different opportunities are equivalent. The sensitivity analysis revealed that a group of robots cannot perform a collective choice if the two shelters are very large or if the size of the group is too large. In the first case, the collective choice is prevented by a dilution effect that restricts the possibilities for the robots to interact and therefore to aggregate. In the second case, the large number of individuals interferes with the collective decision process because of the formation of several

stable aggregates which delay the choice beyond the experiment's duration and might even prevent it. Finally, these results suggest that there exists a range of shelter sizes and group sizes for which a collective decision can emerge from the cockroach aggregation behavior.

3.2 Shelters with Different Sizes

3.2.1 Robotic Experiments

Medium Versus Small Shelters Figure 5a and c summarize the experimental results for the case with a medium and a small shelter. Figure 5a illustrates the temporal dynamics of the number of aggregated robots under the medium and the small shelters. As in the previous section, these dynamics displayed two distinct phases. The first linear growth phase lasted approximately 15 minutes and ended with approximately 70% of the overall population of robots aggregated under the medium shelter, while only 5% was aggregated under the small one. During the second phase the percentage of robots under the medium shelter remained stable at around 70%. At the end of the experiments, $68 \pm 3.2\%$ (mean \pm SE) of the overall population was aggregated under the medium shelter, while $1.5 \pm 1.1\%$ (mean \pm SE) was aggregated under the small one.

Figure 5c illustrates the experimental choice distribution for shelter S_1 (i.e., the medium shelter). This choice distribution displayed a single peak. Ninety-five percent of the experiments ended with more than 80% of the aggregated robots under the medium shelter. All of the experiments ended with more than 60% of the aggregated robots under the medium shelter. The comparison with a random choice distribution was highly significant ($\chi^2 = 87.16$, $p = .0002$, p -value simulated with 10,000 replications). The comparison with the distribution of the identical shelters case was also highly significant (Fisher's exact test, $p < .0001$).

Medium Versus Large Shelters Figure 6a and c summarize the experimental results for the case with a medium and a large shelter. Figure 6a illustrates the temporal dynamics for the number of aggregated robots under the medium and the large shelters. As aforementioned, these dynamics displayed two distinct phases. The first linear growth phase lasts approximately 15 minutes and ended with approximately 60% of the overall population of robots aggregated under the large shelter, and 25% under the medium one. Dur-

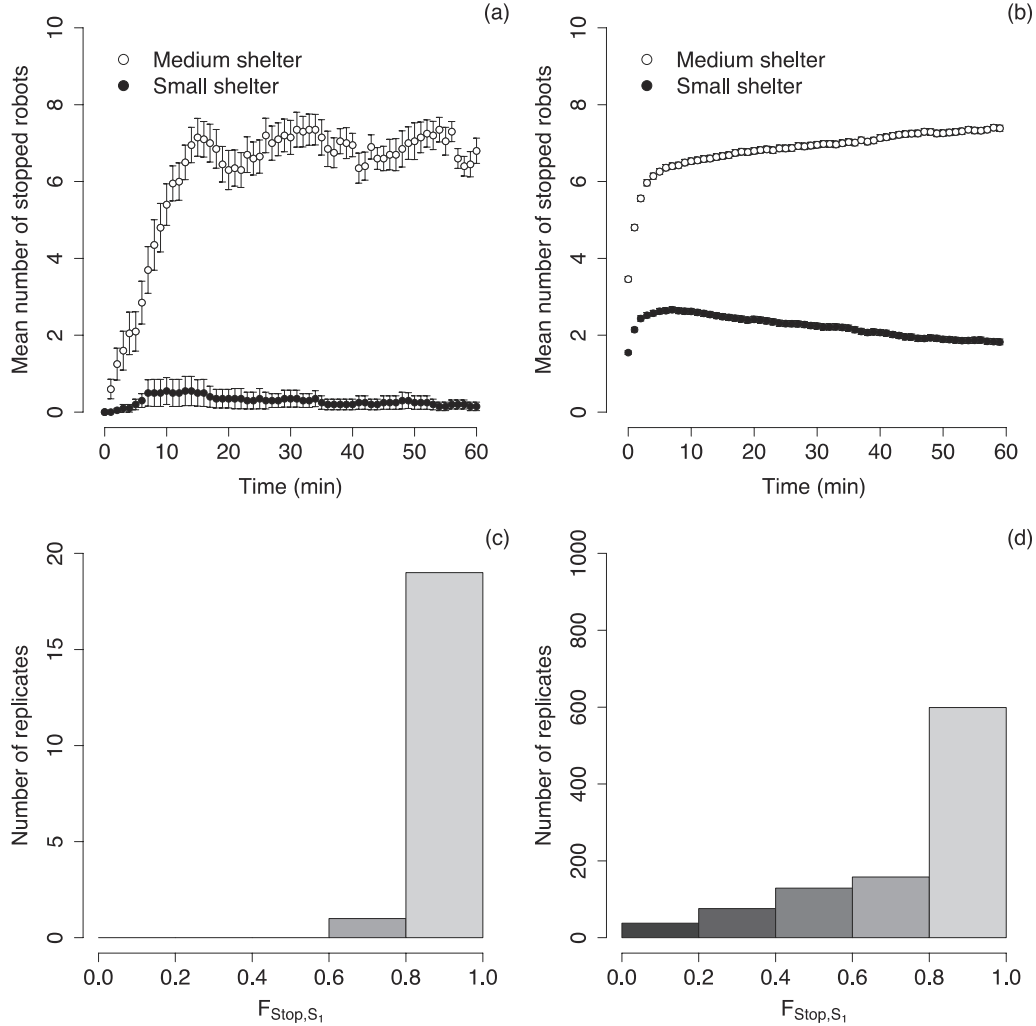


Figure 5 Results of the experiments and the simulations with a medium and a small shelter. **Top:** number of robots aggregated under each shelter per minute. (a) Experimental data ($n = 20$). (b) Simulation data ($n = 1000$). Black dots represent data for the small shelter (radius of 5 cm) and white dots those for the medium shelter (radius of 7 cm). Each dot represents the mean \pm SE **Bottom:** choice distributions. In these distributions, each block represents the number of experiments that ended with a given percentage (0–20, > 20–40, > 40–60, > 60–80, > 80–100%) of stopped robots under the medium shelter (independently of whether it was chosen or not). Extreme values of the distribution (between 0 and 0.2, and between 0.8 and 1) represent experiments that ended with at least 80% of the aggregated robots under the medium shelter (0.8 to 1) or under the small shelter (0 to 0.2, i.e., experiments that ended with less than 20% of the robots under the medium shelter). (c) Experimental distributions ($n = 20$). (d) Simulation distributions ($n = 1000$).

ing the second phase the percentage of robots under the large shelter remained stable around a plateau at 60%. At the end of the experiments, $70.5 \pm 7.6\%$ (mean \pm SE) of the overall population was aggregated under the large shelter, while $17.5 \pm 7.1\%$ (mean \pm SE) was aggregated under the medium one.

Figure 6c illustrates the experimental choice distribution for shelter S_1 (i.e., the medium shelter). This

choice distribution displayed a biased U shape, with 75% of the experiments ending with more than 80% of the aggregated robots under the large shelter and 15% of the experiments ending with more than 80% of the aggregated robots under the medium shelter. The comparison with a random choice distribution was highly significant ($\chi^2 = 256.21$, $p < .0001$, p -value simulated with 10,000 replications). The comparison with

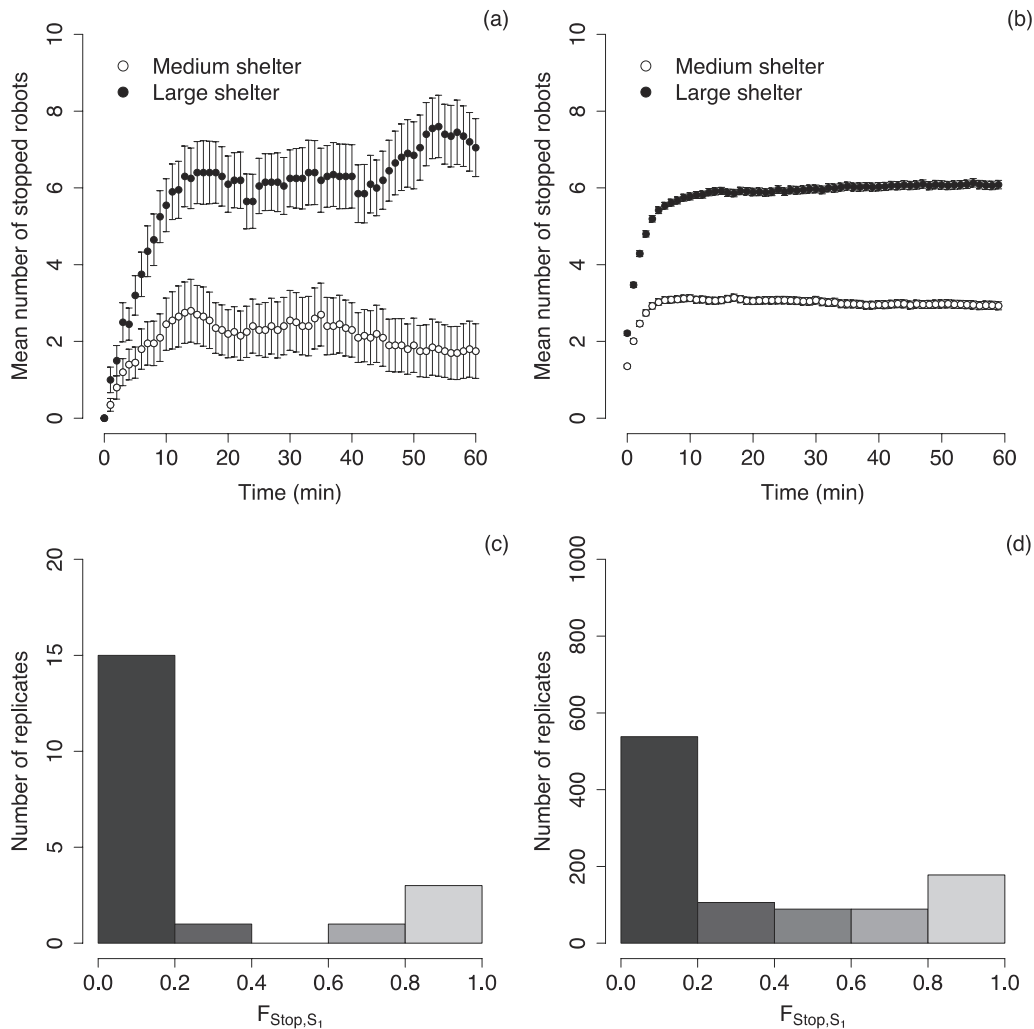


Figure 6 Results of the experiments and the simulations with a medium and a large shelter. **Top:** number of robots aggregated under each shelter per minute. (a) Experimental data ($n = 20$). (b) Simulation data ($n = 1000$). Black dots represent data for the large shelter (radius of 9 cm) and white dots those for the medium shelter (radius of 7 cm). Each dot represents the mean \pm SE. **Bottom:** choice distributions. In these distributions, each block represents the number of experiments that ended with a given percentage (0–20, > 20–40, > 40–60, > 60–80, > 80–100%) of stopped robots under the medium shelter (independently of whether it was chosen or not). Extreme values of the distribution (between 0 and 0.2, and between 0.8 and 1) represent experiments that ended with at least 80% of the aggregated robots under the medium shelter (0.8 to 1) or under the large shelter (0 to 0.2, i.e., experiments that ended with less than 20% of the robots under the medium shelter). (c) Experimental distributions ($n = 20$). (d) Simulation distributions ($n = 1000$).

the distribution of the identical shelters case was also highly significant (Fisher's exact test, $p < .0282$).

3.2.2 Simulator Validation

Medium Versus Small Shelters Figure 5b and d summarize the simulation results for the case with a medium and a small shelter. As for the robotics experiments

(see Figure 5a), the dynamics of the choice displayed in the first minutes illustrated a rapid linear growth in the number of aggregated robots under the medium shelter, followed by a plateau in the rest of the simulation. At the end of the simulations, $73.87 \pm 0.8\%$ of the overall population aggregated under the medium shelter ($75.5 \pm 3.36\%$ in the experiments), while $12.85 \pm 0.5\%$ aggregated under the small one ($1.5 \pm 1.1\%$ in

the experiments). Moreover, the comparison between the simulated (see Figure 5d) and the experimental (see Figure 5b) choice distributions was not significant (Fisher's exact test, $p = .05834$).

Medium Versus Large Shelters Figure 6b and d summarize the simulation results for the case with a medium and a large shelter. As for the robotics experiments (see Figure 6a), the dynamics of the choice displayed during the first minutes illustrated a rapid linear growth of the number of aggregated robots under the large shelter, followed by a plateau during the remaining time. At the end of the simulations, $60.85 \pm 1.11\%$ of the overall population aggregated under the large shelter ($70.5 \pm 7.6\%$ in the experiments), while $29.29 \pm 1.07\%$ aggregated under the medium one ($17.5 \pm 7.1\%$ in the experiments). Moreover, the comparison between the simulated (see Figure 6d) and the experimental (see Figure 6b) choice distributions was not significant (Fisher's exact test, $p = .5351$).

3.2.3 Sensitivity Analysis Figure 7 summarizes the sensitivity analysis in the different shelters case for 10 simulated robots. It represents the fraction of replications ending with at least 80% of the robots aggregated under the shelter with a constant radius ($F_{S_1 \geq 0.8}$), under the shelter with a varying radius ($F_{S_2 \geq 0.8}$) or under both shelters ($F_{S \geq 0.8}$) as a function of the ratio between the radius of the varying shelter and the radius of the constant shelter $\left(\frac{r_{S_2}}{r_{S_1}}\right)$.

As $\frac{r_{S_2}}{r_{S_1}}$ grows from 0 to 7, $F_{S_1 \geq 0.8}$ monotonically decreases, approximately following an exponential decay from 0.984 to 0. $F_{S_2 \geq 0.8}$ is equal to 0 for $\frac{r_{S_2}}{r_{S_1}} < 0.71$, that is, when r_{S_2} is inferior to the minimal known radius of the circle required to house 8 robots (i.e., 80% of the whole group). It then grows and reaches a plateau around 0.55 for $1.5 \leq \frac{r_{S_2}}{r_{S_1}} \leq 2.7$. Finally, $F_{S_2 \geq 0.8}$ decreases as $\frac{r_{S_2}}{r_{S_1}}$ increases. In addition, $F_{S \geq 0.8}$ (the sum of $F_{S_1 \geq 0.8} + F_{S_2 \geq 0.8}$) initially follows the same decay as $F_{S_1 \geq 0.8}$ until $\frac{r_{S_2}}{r_{S_1}} < 0.71$. It then switches to a plateau around 0.6 before continuing the decay for $\frac{r_{S_2}}{r_{S_1}} > 2.7$.

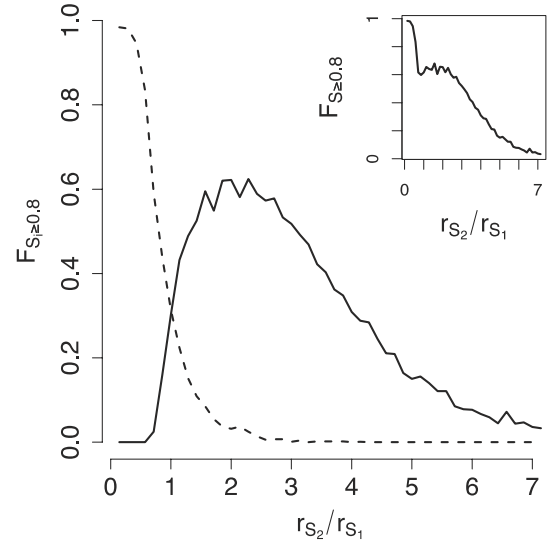


Figure 7 Different shelters case. **Dashed line:** fraction of simulation replications that end with at least 80% of the robots aggregated under shelter 1 ($F_{S_1 \geq 0.8}$) as a function of the ratio between the radius of shelter 2 (the size of which varies, r_{S_2}) and the radius of the shelter 1 (the size of which remains constant, r_{S_1}). **Solid line:** fraction of simulation replications that end with at least 80% of the robots aggregated under shelter 2 ($F_{S_2 \geq 0.8}$) as a function of the ratio between r_{S_2} and r_{S_1} . **Inset:** fraction of simulation replications that end with at least 80% of the robots aggregated under the same shelter ($F_{S \geq 0.8} = F_{S_1 \geq 0.8} + F_{S_2 \geq 0.8}$) as a function of the ratio between r_{S_2} and r_{S_1} . For each value of $\frac{r_{S_2}}{r_{S_1}}$ 1000 simulation replications have been performed with a group of 10 robots.

Together, these three curves lead to the following conclusions. For small ratios, the varying shelter S_2 is too small to house eight robots ($\frac{r_{S_2}}{r_{S_1}} < 0.71$), the constant shelter S_1 is therefore selected in most of the experiments. During this first part, the decrease of $F_{S_1 \geq 0.8}$ is a consequence of the increase of r_{S_2} . As the available space under S_2 increases, the competition between S_1 and S_2 is amplified and the probability for a replication to end with 80% of the robots under S_1 decreases. Once S_2 is sufficiently large to house eight robots ($\frac{r_{S_2}}{r_{S_1}} \geq 0.71$), $F_{S_2 \geq 0.8}$ starts to grow while $F_{S_1 \geq 0.8}$ continues to decrease. $F_{S \geq 0.8}$ reaches a plateau from

this point: the decrease of $F_{S_1 \geq 0.8}$ is balanced by the increase of $F_{S_2 \geq 0.8}$.

Interestingly, $F_{S_1 \geq 0.8}$ and $F_{S_2 \geq 0.8}$ are not symmetrical before and after $\frac{r_{S_2}}{r_{S_1}} = 1$. $F_{S_1 \geq 0.8}$ starts from a value near 1 and goes down to 0, while $F_{S_2 \geq 0.8}$ starts from 0 but only grows until around 0.6 before decreasing. As in the identical shelters case, this final decrease of $F_{S_2 \geq 0.8}$ is mainly caused by the increase of the available space as a consequence of the constant ratio between the surface of the arena and the cumulated surface of the shelters. As r_{S_2} grows the available space under shelter S_2 and outside the two shelters grows. As a consequence, the robot density decreases as the arena size grows. Therefore, the probability of a robot encountering an aggregate and stopping diminishes. This reduces the probability of obtaining a stable cluster under shelter S_2 since moving robots are less likely to stop in existing aggregates.

Note that additional simulations with different group sizes (5, 10, 20, and 50 robots) revealed qualitatively similar results and are therefore not shown here (see, however, Appendix Section A.3 for the results).

3.2.4 Summary of Different Shelters Case If one of the two shelters is bigger than the other, the aggregation behavior is also able to trigger a collective choice. However, this collective choice favors one of the opportunities. In the case of the medium versus the large shelter, the two shelters can be chosen by the robots, but more experiments end with a choice of the large one. In the case of the medium versus the small shelter, the group only chooses the medium one and never chooses the small one. The sensitivity analysis confirms that the choice is biased toward the larger shelter in which the probability of encountering a robot is greater. Moreover, the larger shelter is more often selected if the smaller shelter is not sufficiently large to house the whole population of robots. As in the identical shelters case, there exists a range of shelter sizes for which a collective decision can emerge from cockroach aggregation behavior.

4 Discussion

The restriction to two distinct but identical shelters in the self-organized aggregation behavior described by

Jeanson et al. (2005) enables a group of robots to collectively select one of them. The dynamic of this choice (the evolution of the number of robots under each shelter) is similar to the dynamics of other self-organized decision-making processes (Camazine et al., 2001). This shows that the local amplification that triggers aggregation behavior also works as a mechanism for the collective choice of a shelter: the greater the size of an aggregate under a shelter, the greater the probability that a robot will join the cluster and rest under the shelter. As time goes on, the decreasing number of moving robots (Garnier et al., 2008) brings the global dynamics to a standstill with a majority of the robots clustered under only one of the two available aggregation places.

A disparity in aggregation between the two shelters can be amplified by the collective choice mechanism. The presence of a slight size difference between the shelters biases the final choice toward the bigger one. Interestingly, a similar result has recently been found in a set of experiments with groups of 10, 20, and 30 real cockroaches: they preferentially choose to aggregate under the larger of two shelters (Terramorsi, Sempo, & Deneubourg, 2007). This strengthens the validity of the biological model used in our study to explain the emergence of the collective choice in cockroaches from their aggregation behavior. From the robotic point of view, this implies that a group of robots is able to “sense” and “compare” the size of the shelters during the collective decision process. The group acts as a “larger place detector,” a performance that is beyond the direct scope of the simple aggregation process used in these experiments and that is not explicitly implemented in individual robots.

The influence of a physical characteristic on the final choice has already been reported for other self-organized decision-making processes. For instance, Dussutour, Deneubourg, and Fourcassié (2005) showed that the presence of a wall along one of the paths linking the nest and a food source induces a collective selection of this path by the ant *Lasius niger*. The natural tendency of this ant to follow edges enhances the positive feedback and thus leads to the choice of paths passing along spatial heterogeneities. As another example, the ants *Messor barbarus* preferentially select a dark rather than a light place to aggregate (Jeanson, Deneubourg, Grimal, & Theraulaz, 2004). In this case, ants modulate their recruitment behavior as a function of the quality (dark/light) of the place: the intensity of

the recruitment toward dark places being stronger than toward light places, the former is preferentially selected. But a physical property of the environment can also have an influence through the collective dynamics and without any modulation of the individual behavior. For example, this is what happens when the ant *Linepithema humile* preferentially selects the shortest path between its nest and a food source (Aron, Deneubourg, Goss, & Pasteels, 1990; Goss, Aron, Deneubourg, & Pasteels, 1989; Vittori et al., 2006). Here, ants following the shortest path need less time to go back and forth between the source and the nest. Therefore, they replicate the pheromone trail on the shortest path more often than ants following longer ones. The amplification of the pheromone trail is thus faster on the shortest path which is finally chosen.

The bias in the collective choice of a shelter by the robots (shown here) and the cockroaches (Teramorsi et al., 2007) pertains to this last point. The physical properties of the shelters do not trigger any modulation of the individual behavior that could favor preferential choice of the larger shelter. Rather, individuals have a greater probability of encountering the latter because its periphery is larger, and they spend more time moving under it also because its surface is larger. Together, these two factors increase the probability that an aggregate is first initiated and then amplified under the larger shelter.

Finally, the preference for the larger shelter is increased when the radius of the smaller shelter is close to the minimal known radius of the circle required to house the robots. The experimental results demonstrated that the small shelter, with a radius close to the limit, is never chosen in preference to a medium shelter, while the medium shelter is sometimes chosen in preference to a large shelter. The small shelter can house the robots only if they are arranged according to some particular configurations. Otherwise some of the robots are prevented from entering the shelter by physical obstruction and they remain available to initiate a cluster in the other shelter. This makes the choice of the small shelter an unstable solution in most of the situations and enhances the bias toward choosing the larger shelter.

Computer simulation results were statistically similar to those from the robotics experiments. The sensitivity analyses indicated a range of group sizes and shelter radii that favored the occurrence of a col-

lective decision when the two shelters were of equal size. As in the robotics experiments, the choice is biased toward the larger shelter in the case of shelters with different radii. The choice of the larger shelter is enhanced if the smaller shelter is not large enough to house all the robots.

The sensitivity analyses also revealed that the collective decision mechanism is hindered if the available space inside or outside the shelters is too ample. The probability of a robot encountering an aggregate diminished with the area explored which prevents the self-amplification of cluster size. Aggregation and hence a collective choice are thus unlikely to occur because the density of individuals inside the experimental arena is too small. A similar density-dependent effect was obtained with the deterministic mathematical model proposed by Amé et al. (2006) for a similar experimental setup. An extended analysis of this model (shown in the Appendix) predicts that the robots will not produce a collective choice if the two shelters are much larger than the minimal size required to house the whole population.

Whatever the model used, such dilution effects raise the following question: is the collective choice of a shelter likely to occur in nature where the available space to explore is more important than in our experiments? The dilution effect may be explained by the experimental conditions used by Jeanson et al. (2005) to study the aggregation behavior of *B. germanica* and to build the behavioral model that is used in our work. Experiments with German cockroaches were performed in arenas never visited by the insects and carefully cleaned after each trial. Therefore, the observed exploratory behavior was a random walk with the consequence that the probability of encountering other individuals diminished rapidly with the size of the area explored. In nature, German cockroaches mark their home range with aggregation reinforcing pheromones contained in their feces (Rust et al., 1995) and they mark trails that orient their displacements in preferential directions (Jeanson & Deneubourg, 2006; Miller & Koehler, 2000; Miller, Koehler, & Nation, 2000). They also use visual landmarks and idiothetic cues to establish familiar routes to food sources in their home range (Durier & Rivault, 1999, 2000, 2001; Rivault & Durier, 2004). Together these points suggest that the random exploratory behavior is less frequent in nature than in Jeanson et al.'s (2005) model and that, as a consequence, individual dispersal

is more directed than in our experiments. This should increase the number of interactions between individuals and favor the occurrence of a collective choice of a place to aggregate, provided that several shelters are present and that they are linked by scent trails or not too far from each other.

This observation has an important consequence for the utilization of this collective place selection behavior in groups of robots: it must be coupled with a mechanism that favors interactions between individuals. As with all self-organized processes, its properties mainly rely on the repeated interactions that happen between the lower level components of a system (Camazine et al., 2001). Its efficiency will therefore be decreased if the number of interactions is not maintained at a sufficient level.

The second point revealed by the sensitivity analyses is delayed collective decision making as the number of individuals increases. The greater the number of robots, the more likely the formation of several large, and therefore long-lasting, clusters (more than 10 individuals). The competition between these clusters delays the collective decision process in most of the replications with a large number of robots beyond the experiment's duration of 60 min. It is even possible that no collective decision occurs with groups larger than 40 individuals. An exhaustive analysis of the cockroach aggregation model shows that at stationary state the mean number of aggregates formed by 40 cockroaches is two (data not shown). It is therefore likely that a large population of cockroaches (40 or more individuals) preferentially splits between the different shelters, even if each of the shelters is sufficiently large to house the whole population. This is consistent with several observations regarding the number of *B. germanica* forming a cluster: depending on the kind, size, and quality of the shelters, an aggregate usually includes between 10 and 30 individuals (Rust et al., 1995). Thus, the collective choice mechanism used in our study does a good job of explaining the distribution of cockroaches in natural populations. Moreover, it has been shown that aggregation increases the survival rate of cockroaches, especially at low humidity levels (Dambach & Goehlen, 1999), and also increases rates of both nymphal development and oothecae production in *B. germanica* (Lihoreau & Rivault, 2008). However, there is a limit: group and individual developmental experiments have shown that overcrowding decreases both survival rate and growth rate of *B. ger-*

manica (Rust et al., 1995). Therefore the collective choice mechanism could also have an adaptive value for this insect since it favors the splitting of large populations under different shelters and consequently avoids overcrowding in only one aggregation place.

In a robotics context such a population size dependent splitting behavior will affect the ability of large groups to select a place in the environment. However, this lack of choice could be turned into a simple yet efficient means to spontaneously distribute a large population of robots into subgroups that would simultaneously perform a collective task at different places in the environment. Moreover, we suggest that the tuning of the aggregation parameters should influence the mean size of these subgroups. One could therefore control more or less precisely the number of robots allocated to the different places of interest.

Nevertheless, preserving the collective selection behavior in large groups of robots may remain a desirable property that would require a modification of the current individual behavioral model. Interestingly, the splitting behavior, which depends on group size in robots, is absent from the mathematical mean field model proposed by Amé et al. (2006). The mathematical model instead predicts that the behavior of the group at steady state does not depend on its size. The difference between our model and Amé et al.'s (2006) model lies in the individual behavior that triggers the self-amplification mechanism. In our model, the probability of leaving a cluster depends on the number of perceivable neighbors, which is limited to three neighbors. As stated earlier (see Section 2.4.1), if several sufficiently large clusters appear (which is likely in large populations), they should be very stable. As a consequence, it is unlikely that only one of them eventually captures all the individuals. Such an occurrence of several stable aggregates has also been demonstrated with very similar behavioral models (Nicolis, 2007; Theraulaz et al., 2002). In the model of Amé et al. (2006), however, the probability of leaving a shelter depends directly on the density of all individuals under this shelter. Therefore, the most stable situation occurs when all the individuals are clustered under only a single shelter. The formation of subgroups is hence unlikely to occur with this model, whatever the size of the population. Concerning this point, our model seems more realistic compared with what cockroaches do, but does not scale sufficiently for a robotic application.

To apply Amé et al.'s (2006) model with a large group of robots, the robots should hence be able to individually estimate the density under a shelter. This could easily be performed by counting the number of contacts with other robots encountered while exploring the shelter. Indeed, the rate of encounters with another robot under a shelter is likely to grow with the density of robots under this shelter. For instance the ant *Temnothorax albipennis* successfully uses such a strategy to assess the number of conspecifics in its nest (Pratt, 2005). Note, however, that switching from the counting of the local number of individuals to the estimation of the density under the entire shelter may affect the selection behavior when the group faces two shelters of different radius. As found, cockroaches (Teramorsi et al., 2007) as well as robots implemented with our model preferentially choose the larger of two shelters to aggregate, because the probability of encountering this shelter is greater and favors the initiation of a cluster. Amé et al.'s (2006) model instead predicts that individuals should aggregate under the shelter that allows them to reach a maximal density, provided that the two shelters are sufficiently large to house the whole population (Jean-Louis Deneubourg, personal communication). Thus, this model predicts that the group should select the smaller of two shelters. Here again, our model captures cockroach collective behavior better than Amé et al.'s (2006) model.

In conclusion, our robotics experiments demonstrated that a model initially designed to understand the aggregation behavior of the German cockroach *Blattella germanica* also explains their collective ability to select a place to aggregate among two opportunities scattered in their environment. In a uniform environment, the modulation of the probability to join a cluster, and of the time to stay in the cluster, by the number of proximate neighbors leads to the aggregation of cockroaches (Jeanson et al., 2005) and robots (Garnier et al., 2008). In a heterogeneous environment where certain places favor the clustering of individuals, the same amplification mechanism leads our robots to aggregate at only one of these places. Moreover, the collective decision is influenced by the available space at the different places and by the probability of encountering these places while the robots explore the environment. A set of simulations calibrated from the robotics experiments revealed that this collective choice behavior was sensitive both to the spaces available to explore and to aggregate in, and to the size of

the population involved in the aggregation process. Interestingly, these results match well several observations about the real collective behavior of this cockroach species and about its dispersion in natural environments.

A Appendix

A.1 Behavioral Model

The behavioral model we use in this work is an extension of the aggregation model described by Jeanson et al. (2003, 2005) and implemented in robots by Garnier et al. (2008). The original behavioral model was developed from experiments with first instar larvae of the German cockroach, *Blattella germanica*. In its natural environment, *B. germanica* forms dense aggregates of individuals of both sexes and all developmental stages especially at low external humidity (Dambach & Goehlen, 1999; Ledoux, 1945). The original behavioral model explains the mechanism of self-organization that leads to this aggregation behavior. In the extended model, the aggregation behavior is restricted to dark places in the environment.

The detailed description of the extended model can be broken down into two parts: displacement and stopping behavior. See Figure A.1 for a schematic description of the behavioral model. All model parameter values are listed in Table A.1.

A.1.1 Displacement

The experimental arena is subdivided into two zones: a central zone and a peripheral zone. The peripheral zone is an external ring inside which a robot detects the arena wall. The central zone corresponds to the rest of the arena.

In the central zone, a robot moves at speed v_c according to a random walk, that is a series of straight line moves that follow an exponential distribution of mean l , interrupted by rotations in which angles are uniformly distributed in $[-180; 180]$ degrees (isotropic distribution). Alice robots can only handle integers, therefore we used random number generators based only on integers. Uniform random numbers were generated with a "Quick & Dirty" algorithm (Press, Teukolsky, Vetterling, & Flannery, 1992). Exponential random numbers with mean l were created from a uniform ran-

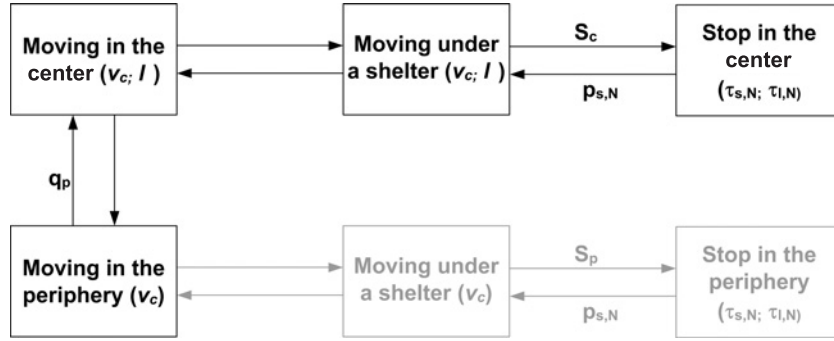


Figure A.1 Schematic representation of the behavioral model. Parameters are: speed in the center v_c , speed in the periphery v_p , mean free path l , rate to quit the periphery q_p , rate to stop in the center s_c or periphery s_p , probability to be in the short stop state $p_{s,N}$ with mean short stopping time $\tau_{s,N}$ and mean long stopping time $\tau_{l,N}$ (as a function of the N stopped neighbors). The transition probabilities from moving in the center to moving in the periphery and between moving in the center or the periphery and moving under a shelter are not directly encoded in the model since they are direct consequences of the individual displacement. Moving and stopping under a shelter in the periphery are displayed in gray because these situations are taken into account in the model, but cannot occur inside our experimental setup (shelters are never placed close enough to the periphery of the arena). The parameter values are listed in Table A.1.

dom number r generated as previously explained and transformed to $-\log(r)l$ with an algorithm using only integers (see Ahrens & Dieter, 1972, for the algorithm). Letting the robot move or turn at maximum speed we computed from these random numbers the time (in ms, which is the unit of the internal clock in an Alice robot) that it should move straight forward or turn. This random walk is continued until an Alice detects an arena wall with its infra-red sensors.

When a robot detects a wall and enters the peripheral zone, it switches into a wall-following behavior (provided with the pre-programmed sensory-motor behaviors of Alice robots, see Caprari, 2003). The robot aligns its body with the wall and moves at speed v_p in order to keep contact with the wall. The time a robot follows the wall is also exponentially distributed with mean τ_{Exit} and was computed as described above. Upon completion of this wall-following path the robot returns to the central zone with a random angle drawn uniformly between 17 and 78 degrees. This is an approximation to the log-normal angle distribution measured by Jeanson et al. (2003) the computation of which would exceed the capacities of Alice robots.

During its displacement, a robot can enter a shelter. The shelter triggers a significant drop in the background infrared light intensity detected by the robot. This drop informs the robot that it is under a shelter. The robot will not modify its moving characteristics and continues its displacement according to the ran-

dom walk rules. However, when under a shelter, the robot can decide to stop, which can not occur outside the shelter. This rule restricts the aggregation behavior to the dark places and is the only addition to the original aggregation model from Jeanson et al. (2005) and Garnier et al. (2008).

A.1.2 Stopping Behavior

The stopping behavior is only possible under a shelter and depends on the number N of neighbors that a robot detects through its local infra-red communication (s_N , $0 \leq N \leq 3$). Each robot broadcasts with its infrared emitters two robot-specific identification numbers: an odd one if it is moving (movement number) and an even one if it is stopped (stop number). This emission can be read by other robots up to a distance of ≈ 4 cm. Each robot can thus detect the number of stopped robots in its immediate neighborhood.

The rate of stopping is constant per unit time (memory-less process); the above displacement is thus interrupted every 500 ms and a random number uniformly distributed between 0 and 1 is drawn to decide whether or not the robot should stop. If this number is less than a given threshold (s_c if the robot is in the center, s_p if it is in the periphery, s_N if the robot perceives N neighbors), then the robot stops.

Once stopped, the robot decides whether the duration of the stop is short or long. The probability $p_{s,N}$ of

Table A.1 Individual behavioral parameters of the Alice robots as measured by Garnier et al. (2008). v_c : speed in the center of the arena. l : mean free path in the center of the arena. v_p : speed in the periphery of the arena. τ_{exit} : mean time a robot follows a wall. s_c : probability to spontaneously stop in the center of the arena. s_p : probability to spontaneously stop in the periphery of the arena. s_N : probability to stop in the presence of N ($N > 0$) stopped robots. $\tau_{s,N}$: mean duration of a short stop in the presence of N ($N \geq 0$) stopped robots. $\tau_{l,N}$: mean duration of a long stop in the presence of N ($N \geq 0$) stopped robots. $p_{s,N}$: probability to perform a short stop in the presence of N ($N \geq 0$) stopped robots.

Parameter	Value
v_c ($cm\ s^{-1}$)	3.97
v_p ($cm\ s^{-1}$)	3.68
s_c (s^{-1})	0.026
s_p (s^{-1})	0.074
l (cm)	11.35
τ_{exit} (s)	9.25
$\tau_{s,0}$ (s)	7.52
$\tau_{l,0}$ (s)	626
$p_{s,0}$	0.943
s_1 (s^{-1})	0.30
$\tau_{s,1}$ (s)	11.39
$\tau_{l,1}$ (s)	733
$p_{s,1}$	0.62
s_2 (s^{-1})	0.40
$\tau_{s,2}$ (s)	9.98
$\tau_{l,2}$ (s)	713
$p_{s,2}$	0.27
s_3 (s^{-1})	0.41
$\tau_{s,3}$ (s)	6.64
$\tau_{l,3}$ (s)	910
$p_{s,3}$	0.09

performing a short stop varies according to the number N of neighbors a robot can detect ($0 \leq N \leq 3$, the probability to perform a long stop is equal to $1 - p_{s,N}$). The robot thus draws a random number uniformly distributed between 0 and 1 to decide whether it will be a short stop (number inferior to $p_{s,N}$) or a long stop (number superior to $p_{s,N}$).

The stop time follows an exponential distribution with a mean depending on N and on the state of the stop (short stop, mean stop time $\tau_{s,N}$; long stop, mean stop time $\tau_{l,N}$).

If the number of stopped neighbors changes during a robot's stop, the robot has to modify the duration of its halt according to the new number of neighbors. Because we deal with a memory-less process, the time the robot has to remain stopped is independent of the time it already spent in this state. Consequently when the number of stopped neighbors changes the robot only draws a new stop time from the appropriate exponential distribution. Note that the robot remembers whether the stop state is short or long.

Once the stop time is elapsed the Alice continues its displacement either with a random walk (center) or a wall-following behavior (periphery).

A.2 Bifurcation Diagram for the Binary Choice of a Shelter in Robots

Amé et al. (2006) give a system of differential equations describing the dynamical choice of a shelter in cockroaches. This system yields different qualitative collective behaviors, depending on the number and size of available shelters. In the case of a binary choice between two shelters of the same size, Amé et al. (2006) provide the bifurcation diagram of the collective choice predicted by the model. Taking the reference shelter size as the size that can hold the whole group, they explored the collective choice for shelter sizes ranging from 0 to 2.5 times the reference size. They showed that all individuals gather under a unique shelter, provided that the shelter size is larger than the reference size (Amé et al., 2006, figure 1). Here, we extend this diagram to greater size differences of the shelters, and show that the collective choice eventually collapses for larger shelters. This collapse can be attributed to the decreasing density of individuals under the shelters, which becomes too low to trigger a self-organizing process.

Let P_i be the proportion of individuals under the shelter i , and P_e the proportion of individuals outside the shelters. Following Amé et al. (2006), the dynamics of the collective choice between two identical shelters follows:

$$\frac{dP_i}{dt} = \mu P_e \left(1 - \frac{P_i}{S}\right) - \frac{\theta P_i}{1 + \rho \left(\frac{P_i}{S}\right)^n} \quad i = 1, 2$$

$$1 = P_1 + P_2 + P_e$$

with S the carrying capacity of the shelters (ratio of shelter sizes over the reference size), μ the maximal kinetic constant for entering a shelter, θ representing the shelter quality, and ρ a reference surface ratio for estimating carrying capacities.

The stationary states are found by simply solving (see details in Amé et al., 2006):

$$\frac{dP_i}{dt} = 0 \quad i = 1, 2$$

Setting

$$\mu = 0.001 \text{ s}^{-1}$$

$$\theta = 0.01 \text{ s}^{-1}$$

$$\rho = 1667$$

$$n = 2$$

we found the complete bifurcation diagram shown in Figure A.2 which shows that no collective choice occurs for $S > 6$.

A.3 Shelter with Different Sizes: Sensitivity Analysis with Different Group Sizes

In the different shelter case, we performed with simulations a sensitivity analysis where a group of 10 simulated robots was confronted with two shelters, one of fixed size (7 cm radius) and one which size varied from 1 cm to 50 cm (i.e., from 0.14 to 7.14 times the radius of the fixed size shelter) by steps of 1 cm. To assess the influence of the group size on this sensitivity analysis, we performed additional sets of simulations with groups of 5, 20, and 50 robots. We scaled the radius of the fixed size shelter so that the ratio between its area and the minimal area occupied by the group remains constant. We varied the radius of the

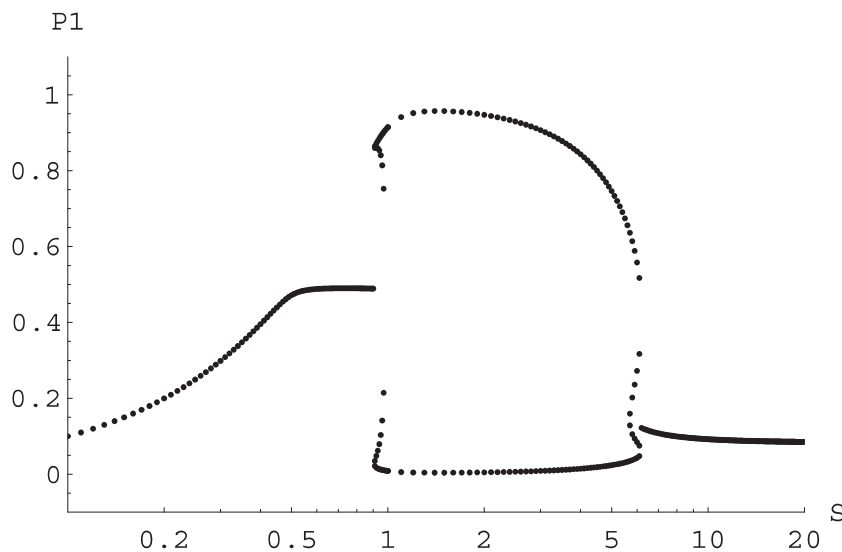


Figure A.2 Bifurcation diagram for the collective choice between two identical shelters. P_1 is the proportion of individuals under the shelter 1 and S is the normalized carrying capacity of the shelters (which corresponds to the ratio of shelter size over the reference size). Only stable stationary states are reported. Note that a collective choice only occurs between $S = 1$ and $S = 5$.

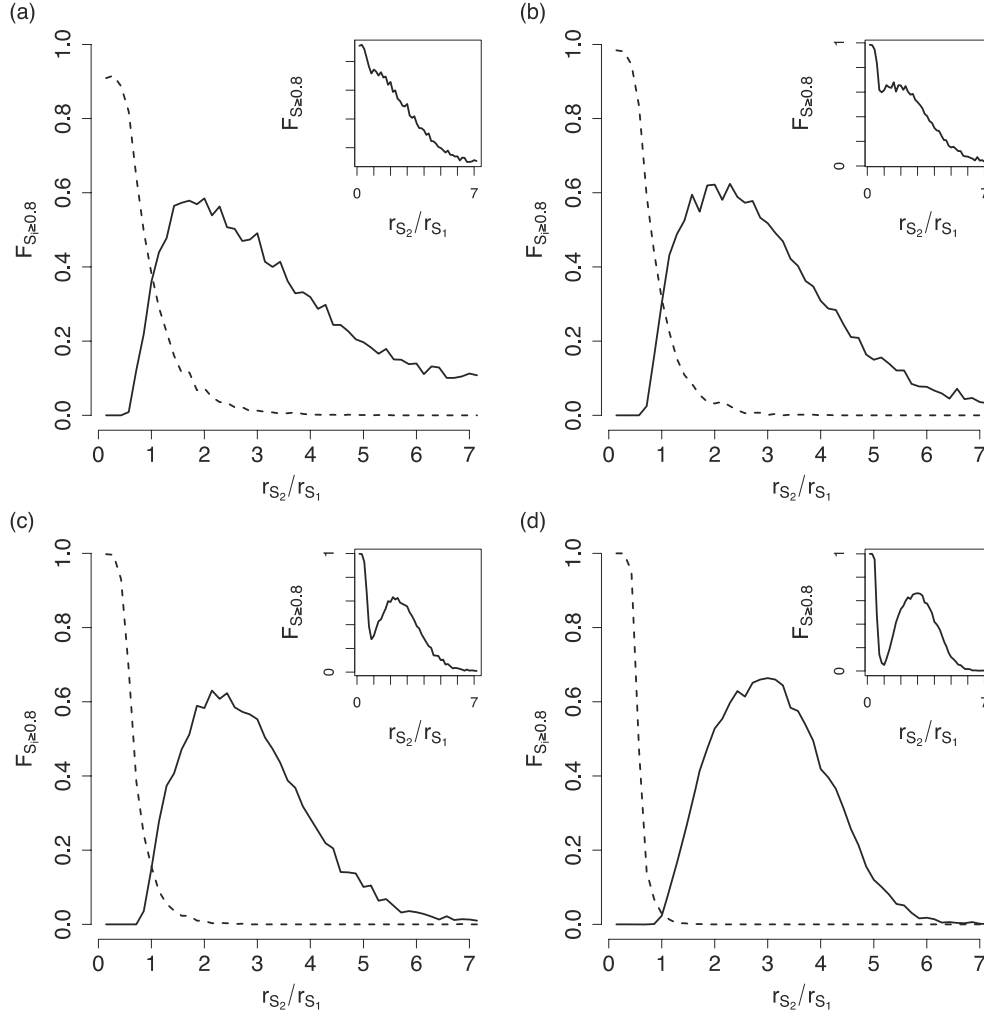


Figure A.3 Different shelters case. **Dashed line:** fraction of simulation replications that end with at least 80% of the robots aggregated under the shelter 1 ($F_{S_1 \geq 0.8}$) as a function of the ratio between the radius of the shelter 2 (which size varies, r_{S_2}) and the radius of the shelter 1 (which size remains constant, r_{S_1}). **Solid line:** fraction of simulation replications that end with at least 80% of the robots aggregated under the shelter 2 ($F_{S_2 \geq 0.8}$) as a function of the ratio between r_{S_2} and r_{S_1} . **Inset:** fraction of simulation replications that end with at least 80% of the robots aggregated under the same shelter ($F_{S \geq 0.8} = F_{S_1 \geq 0.8} + F_{S_2 \geq 0.8}$) as a function of the ratio between r_{S_2} and r_{S_1} . For each value of $\frac{r_{S_2}}{r_{S_1}}$ 1000 simulation replications have been performed with a group of (a) 5, (b) 10, (c) 20, and (d) 50 robots.

varying size shelter from 0.14 to 7.14 times the the radius of the fixed size shelter.

Results of this sensitivity analysis are displayed in Figure A.3. Whatever the size of the group, its behavior remained qualitatively identical to what was described in Section 3.2.3. The only quantitative difference occurred when the radius of the varying shelter

got close to the radius of the constant shelter. In this case, the fraction of simulation replications that ended with at least 80% of the robots aggregated under the same shelter dramatically decreased with the group size. This is in fact exactly the same effect that was already observed in Section 3.1.3 with the sensitivity analysis in the identical shelter case.

Note

1 <http://www.ehl.cz/pic/>

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