

Collegial decision making based on social amplification leads to optimal group formation

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Group-living animals are often faced with choosing between one or more alternative resource sites. A central question in such collective decision making includes determining which individuals induce the decision and when. This experimental and theoretical study of shelter selection by cockroach groups demonstrates that choices can emerge through nonlinear interaction dynamics between equal individuals without perfect knowledge or leadership. We identify a simple mechanism whereby a decision is taken on the move with limited information and signaling and without comparison of available opportunities. This mechanism leads to optimal mean benefit for group individuals. Our model points to a generic self-organized collective decision-making process independent of animal species.

collective behavior | nonlinear dynamics | self-organization

The fundamental ecological issue of determining the distribution of animal group sizes has traditionally been approached by models that assume that individuals possess perfect information about alternatives and that there is no social effect on the decisions. Ideal free-distribution models predict that the distribution of organisms between resource sites will be one that maximizes individual benefit, given the constraints of competition between conspecifics (1). Group-membership games are applied to aggregation economies, where cooperation among conspecifics enhances resource harvesting, and, therefore, individuals in groups are more efficient than solitary conspecifics (1). These categories of models do not discuss the decision mechanisms used by animals. However, expected outcomes of these models probably depend on individual decision-making mechanisms (2–5).

For group-living animals, decision making depends on both social interactions and assessment of environmental opportunities. The important questions concerning the collective decision-making mechanisms include determining which group members induce the decision and whether it precedes action (4–7). Networks of interactions and leadership can play an important role in such context (5, 8–10). Some mechanisms require that a small number of individuals foresee the possibilities and inform their conspecifics (11, 12). Whether this explanation holds for groups of insects, fishes, and birds constrained by crowding effects, range of communication, limited cognitive abilities, and limited signaling capabilities can be questioned.

Here, we address these two fundamental issues in collective decision making: (i) how individuals induce the decision and (ii) how to cope with crowding effects. We focus on the collective choice of shelters or safe resting places that are important resources for many gregarious species of cockroaches, in particular.

Results

We report an experimental and theoretical study of groups of cockroaches (*Blattella germanica*) tested in a circular arena (see Fig. 1A) with identical shelters. The “cockroaches-shelter” system is well adapted to study collective decision making because it provides an interplay between competition for the resources,

which have a limited carrying capacity, and cooperation, whereby individuals aggregate. This interplay allows us to investigate the relationship between behavioral mechanisms and optimality.

In our experimental setup, individuals have no *a priori* information about resource distribution and decide only between staying in a patch and leaving it to search for another. We take into account conspecific attraction for individuals already in a group that affects their probability of leaving to explore and the crowding effect that influences their decision to join the encountered group.

Model for Collective Decision Making. Site selection by cockroaches results from shifts between resting in shelters and exploration of the arena by the insects. We extend previous studies (13–14) and, on a larger data set, we validate a dynamical model of aggregation, based on the behavior of individual cockroaches (see *Supporting Materials and Methods*, which is published as supporting information on the PNAS web site). Each individual in shelter i has a probability Q_i (inverse of resting time estimated experimentally from the resting time distribution) to leave it and to start to explore. Each exploring cockroach has a probability to encounter and to join site i (R_i). Experiments show that Q_i decreases with the number of individuals x_i present in shelter i according to the following equation:

$$Q_i = \frac{\theta}{1 + \rho \left(\frac{x_i}{S}\right)^n} \quad [1]$$

Eq. 1 formulates the interindividual attraction effect and evaluates the probability of leaving a shelter according to its physical characteristics and its occupation level. Parameter θ depends on shelter quality. The maximum probability of leaving a shelter per unit of time is observed with solitary individuals. S is the carrying capacity of the shelter, i.e., the number of individuals that can rest in the shelter. Parameter ρ is a reference surface ratio for estimating carrying capacities. When $n > 1$, the social interactions lead to a threshold response in the residence time as a function of conspecifics presence.

The probability for an exploring cockroach to join site i (R_i) decreases with linear crowding effect:

$$R_i = \mu \left(1 - \frac{x_i}{S}\right) \quad [2]$$

Parameter μ represents the maximal kinetic constant for entering a shelter. R_i decreases with the ratio between the

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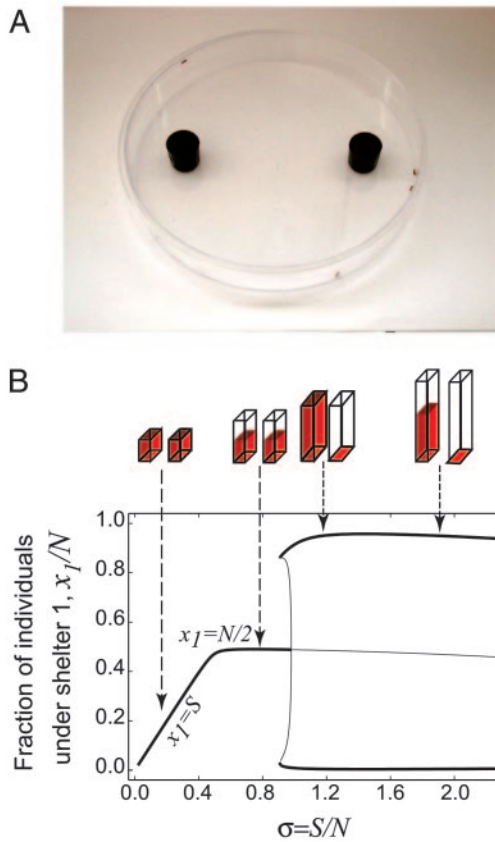


Fig. 1. Experimental setup and bifurcation diagram of the collective choice predicted by the model. (A) Choice tests with groups of cockroaches were made in Petri dishes (14 cm) with small plastic caps for shelters. Numbers of individuals in each shelter were recorded during the resting period 24 h after the beginning of the test. (B) Steady states of Eqs. 3 and 4, giving the fraction of individuals in one shelter as a function of the ratio of the carrying capacity and total individual number σ with the measured values $\mu = 0.001 \text{ s}^{-1}$, $\theta = 0.01 \text{ s}^{-1}$, $\rho = 1,167$, $n = 2$. The steady states and their stability are solved numerically with MAPLE, see text for parameter values. Thick line, stable state; thin line, unstable state. Only one of the shelters is represented for symmetry reason. Above the graph, the corresponding shelter-filling outcome. When $\sigma < 1$, only one solution exists, corresponding to an equal number of individuals in each shelter. When $\sigma < 1/2$, the individuals fill the two shelters up to their maximum ($x_1 = x_2 = S$) When $\sigma > 1/2$, a plateau value is reached corresponding to equipartition of the individuals ($x_1/n = x_2/n = 1/2$). When $\sigma > 1$, three solutions exist, among which one is unstable and corresponds to equipartition, and the two stable states correspond to all individuals in one of the shelters i.e., [$x_1 \approx 0$; $x_2/N \approx 1$; $x_e \approx 0$] or [$x_1/N \approx 1$; $x_2 \approx 0$; $x_e \approx 0$].

number of individuals present on site i (x_i) and its carrying capacity (S).

This model is based on observations showing that no long-range interactions among cockroaches occur (13–15). Neither chemical marking nor memory effect were significant because, under our experimental conditions, the cockroaches were placed in a new environment free of chemical traces laid by conspecifics for a short time (24 h) and were surrounded by a uniform enclosure, preventing cockroaches from using spatial elements beyond the setup (15).

The differential equations describing the time evolution of the number of individuals on each site (x_i) is:

$$\frac{dx_i}{dt} = \mu x_e \left(1 - \frac{x_i}{S}\right) - \frac{\theta x_i}{1 + \rho \left(\frac{x_i}{S}\right)^n} \quad i = 1, \dots, p \quad [3]$$

$$N = x_e + \sum_{i=1}^p x_i, \quad [4]$$

where x_e is the population outside the shelters and p is the number of shelters. When all of the shelters are qualitatively identical, their parameters are equal. All their values are estimated experimentally ($n = 2$, $\theta = 0.01 \text{ s}^{-1}$, $\rho = 1667$, and $\mu = 0.001 \text{ s}^{-1}$; see refs. 13 and 14, and *Supporting Materials and Methods*). The parameter σ , defined as the ratio S/N , measures the carrying capacity expressed as a fraction or a multiple of the total population N . To account for experimental fluctuations (which can be large because of a small number of individuals), we also performed stochastic simulations of the model (13).

Site Selection with Two Sites ($P = 2$). For two shelters ($P = 2$) with small carrying capacities ($S < N/2$ or $\sigma < 1/2$), the model predicts that individuals fill the two shelters up to their maximum ($x_1 = x_2 = S$), and the remaining individuals stay outside (Fig. 1B). Remarkably, when the carrying capacity of each shelter exceeds half the population ($n > S > N/2$ or $1 > \sigma > 1/2$), the shelters are no longer saturated, but individual equipartition between the two shelters remains ($x_1 = x_2 = N/2 < S$, Fig. 1B, plateau branch). Experiments with two shelters and $1 > \sigma > 1/2$ confirm the model predictions. The most frequent distribution corresponds to an equal number of cockroaches in each shelter ($x_1 = x_2 = N/2$) (Fig. 2 A and B, blue bars). Thus, the possible solution of saturating one of the shelters and then placing the surplus in the second shelter is not that produced at the group level. The model demonstrates that this effect is a direct consequence of the linear crowding effect (see Eq. 2).

When S increases and becomes larger than the size of the total population ($S > N$ or $\sigma > 1$), the model predicts two new emerging stable solutions corresponding to almost the entire population in one shelter, leaving the second shelter empty and no individuals outside. The site that receives the entire population is chosen randomly. Equipartition between the two sites still exists but is unstable. Experiments confirm that for large shelters ($\sigma > 1$) nearly all individuals aggregate in one of the shelters, the other remaining empty (Fig. 2 A and B, blue bars). Indeed, the experiments follow a bifurcation pattern that quantitatively matches the stochastic simulations of the model.

Site Selection with More Than Two Sites ($P > 2$). Using the model, we investigated the influence of the numbers of the shelters on the pattern formation. When the number of shelters is larger ($P > 2$, Fig. 3), and the total carrying capacity of the shelters is below the size of the population ($S < N/p$ or $\sigma < 1/p$), the individuals tend to use the scarce available space as much as possible, saturating the sites, and the remaining individuals stay outside.

When the shelter sizes increase ($N/p < S < N$ or $1/pv < \sigma < 1$), a structured cascade of stable solutions appears as a function of σ . The partitions correspond, respectively, to N/p in p , $N/(p-1)$ in $p-1$, $N/(p-2)$ in $p-2$ of the p available sites. The population does not use all of the available shelters as their carrying capacity increases, and, among the selected sites, all groups are of equal size. The plateau value of N/p at which the population stops saturating the occupied shelters starts when the total carrying capacity of the shelters is equal to the size of the population ($S = N/p$). When $N/(p-i-1) > S > N/(p-i)$, the population occupies $p-i$ shelters, and i shelters remain empty. For high values of S ($S > N$), whatever the number of shelters, only one shelter is selected randomly (with a frequency of $1/p$), and it catches the entire population.

For example, the solution made by 50 cockroaches with three shelters having a carrying capacity of 40 each, is: 25 cockroaches

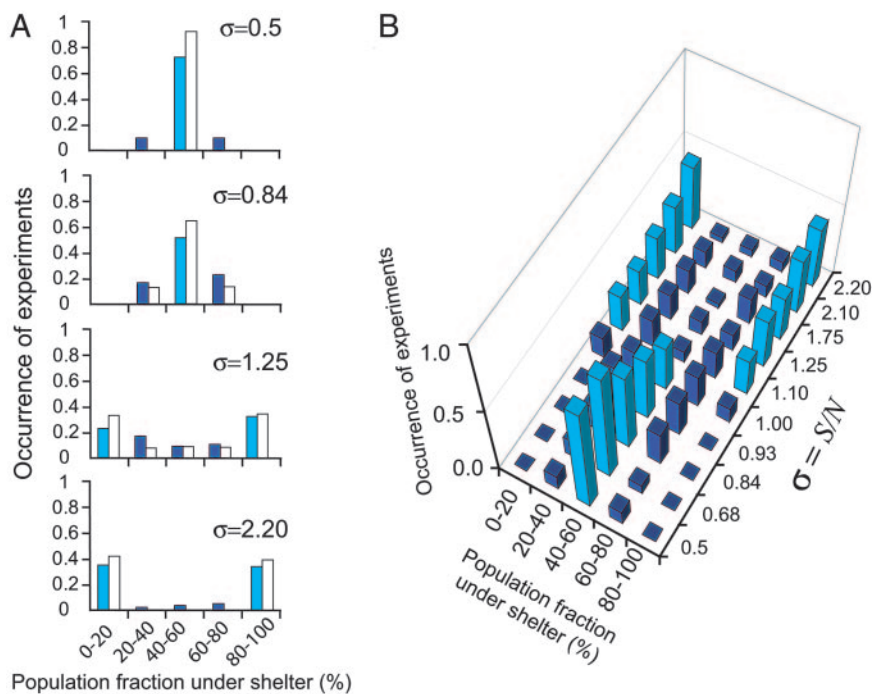


Fig. 2. Experimental individual distributions among shelters and bifurcation diagram. We report on 263 experiments for 10 combinations of N and S that were tested corresponding to 10 different values of the ratio σ . Three values of N and six values of S were used. Blue bars represent the experimental observed frequency of individual distributions for each σ value, related to the population fraction in shelter 1. Light blue bars correspond to the highest experimental frequencies. (A) White bars predicted steady-state distribution by stochastic simulations of the model. The four values of σ correspond to arrows in Fig. 1B. For $\sigma = 0.5$ and $\sigma = 0.84$, i.e., before the bifurcation point predicted in Fig. 1B, the observed distributions are equipartitioned between the two shelters i.e., the class 40–60%; meaning that half of the individuals are in shelter 1, which is the distribution predicted by the model. Because no individual remained outside, the other half was in the other shelter. The predicted plateau value of equipartition is observed experimentally. The possible solution of filling first one shelter and then the other shelter is not selected. Above the bifurcation, for $\sigma = 1.25$ and $\sigma = 2.20$, the most frequently observed distribution corresponds to all individuals selecting the same shelter. The highest observation frequencies are classes 0–20% or 80–100%, with equal observation frequency. This means that nearly all of the individuals were either in shelter 1 or in shelter 2 and that the choice between them is random. (B) Experimental bifurcation diagram, as a function of σ , in quantitative agreement with the model.

in one shelter, 25 in the second shelter, and none in the third. This solution is adopted despite the possibility of filling up one shelter to its maximum, one of the shelters (up to 40), and leaving the surplus individuals (the remaining 10) in another shelter. If the capacity of each shelter is >50 , only one is occupied by all of the cockroaches.

This collective choice is induced by the threshold response in the residence time according to the presence of conspecifics. If $n = 1$, i.e., in absence of this threshold, although social interactions remain, the model shows that the choice disappears and individuals are distributed equally between the shelters in all cases.

Optimality of the Collective Choice. Adaptive value and cost-benefit associated to the gregarious behavior referring to the Allee effect have been widely discussed and for many organisms, from bacteria to mammals (16). Under some circumstances, individuals improve their survival potential by modifying their local environment by aggregating (17). In situations where the animals have to choose among identical resource sites, and there is no cost associated with competition at the site, the highest individual benefit is reached when all individuals are aggregated at the site.

In a patchy environment, the benefit also depends on the patch quality that individuals are visiting or exploiting. The intrapatch competition among individuals for resources favors their dispersion and limits the size of the clusters and benefits from gregariousness.

Ideal free-distribution theory provides a framework to study

the effects of density-dependent resource competition on distribution of individuals or habitat selection (1). This framework predicts equal partition of individuals among identical resources. In our experiments, such distributions are observed only for a specific range of the control parameter (σ). Rather, the experiments are in full agreement with our mechanistic model (Eq. 3).

Aggregation reduces different physical stresses, such as predation, or increases food intake. Under these conditions, individual benefit A , because of the gregarious behavior, increases with the group size x , i.e., $dA/dx > 0$. For equivalent sites, including the observed cooperative effect (i.e., $n \geq 1$, see *Supporting Materials and Methods*). We consider for shelter i the following revenue function:

$$A_i = \left(1 + \rho \left(\frac{x_i}{S} \right)^n \right). \quad [5]$$

Under our experimental conditions, the resources are the number of shelters and their carrying capacity. Groups form by accretion, and the probability that an individual joins a group (R) decreases with the level of occupation of the shelter (x) ($dR/dx < 0$, see Eq. 2) because of crowding effects. This decrease of R corresponds to a competition among individuals. Therefore, two density-dependent effects control the mean individual benefit: the advantage related to the gregarious behavior itself increasing with the cluster size, and the probability of having access to the resource decreasing with the density.

Taking into account the cost of crowding, which reduces the probability of joining a shelter (Eq. 2), the mean benefit per individual with p shelters is:

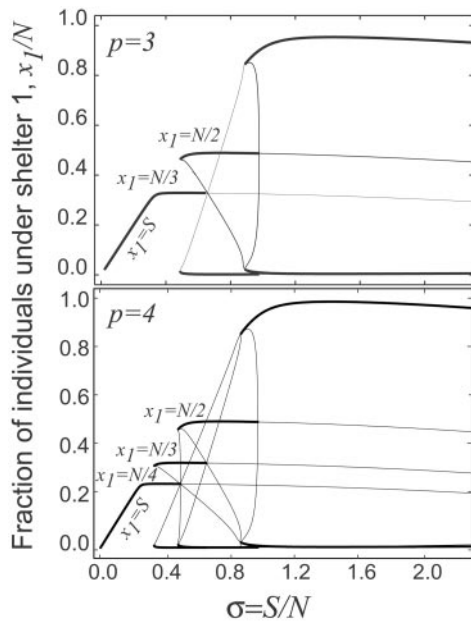


Fig. 3. Bifurcation diagrams showing the fraction of individuals in one shelter, (x_1) in relation to σ with the measured values $\mu = 0.001 \text{ S}^{-1}$, $\theta = 0.01 \text{ S}^{-1}$, and $\rho = 1167$; $n = 2$. Panels show examples for $P = 3$ and $P = 4$ shelters; thin lines, unstable states; thick lines, stable states. For $P = 3$ and for low values of S , the only stable solution is equipartition of individuals among the three shelters ($x_1 = x_2 = x_3$). When S increases ($S \approx N/2$), this state becomes unstable. The stable branch corresponds to solutions where the individuals are equally distributed only among two of the three shelters, the last one remaining empty. For $S > N$, two branches for x_1 are stable, corresponding to the solution where only one shelter harbors all of the individuals and the two others are, therefore, empty ($(x_1 \approx N, x_2 \approx x_3 \approx 0)$; $(x_1 \approx x_3 \approx 0, x_2 \approx N)$; $(x_1 \approx x_2 \approx 0, x_3 \approx N)$). The branches corresponding to an equal distribution between two or three shelters are unstable. For $P = 4$: compared to the previous case, one more stable branch occurs, corresponding to equipartition among the four shelters. When S increases, the cascade of new stable states corresponds to equipartition among three or two shelters. When $S > N$, the only stable state corresponds to one of the shelters harboring all of the individuals. During the emergence of steady states, zones of coexisting stable states are observed.

$$B = \frac{\mu}{N} \sum_{i=1}^p x_i \left(1 + \rho \left(\frac{x_i}{S} \right)^n \right) \left(1 - \frac{x_i}{S} \right). \quad [6]$$

We assume that the benefit outside a shelter $A_e = 0$.

Eq. 6 may also be expressed as a function of $f_i = x_i/N$, the fraction of the population in shelter i and $\sigma = S/N$. B can be nondimensionalized by dividing by the time constant μ , and, after this transformation, B depends mainly on parameter σ :

$$B = \frac{1}{N} \sum_{i=1}^p f_i \left(1 + \rho \left(\frac{f_i}{\sigma} \right)^n \right) \left(1 - \frac{f_i}{\sigma} \right). \quad [7]$$

When $P = 2$, an equal distribution of the population between both shelters ($f_1 = f_2 = 0.5$) always corresponds to an extremum of B . When $\sigma < 1$, i.e., $S < N$, the carrying capacity of one shelter is below the size of the total population (Fig. 4A). In this case, B is maximum for $f_1 = 0.5 (= f_2)$. When $\sigma > 1$ ($S > N$), B is minimum for the equal distribution. The optimal benefits are reached for asymmetrical distributions between both shelters ($f_1 > f_2$ or $f_2 > f_1$). Moreover, as σ increases, the asymmetry of the distribution corresponding to the maximum of the benefit becomes larger. This means that one of the shelters is favored over the other. When $\sigma > 1.2$, the

highest benefits are reached for an aggregation of all of the individuals in the same shelter ($f_1 = 1, f_2 = 0$) or ($f_2 = 0, f_1 = 1$). This preference is due to the dynamics of the process and not to a difference in shelter quality, because both are equal. Hence, the shelter that is selected is chosen randomly with a probability of 0.5, as shown by the model and the experimental data.

Comparing Fig. 4A to Figs. 1 and 2, the optimal benefits correspond to the stable solution of the model. Indeed, for $\sigma < 1$, the equipartition: $f_1 = f_2$ for which B is optimal is a stable solution. A bifurcation occurs $\approx \sigma = 1$, and then the system presents three steady states: equipartition between the shelters and two asymmetrical distributions. The equipartition of individuals is unstable, and B is a minimum. The two other solutions are stable states and correspond to the values ($f_1 = 1, f_2 = 0$) or ($f_2 = 0, f_1 = 1$) that correspond to the optimal benefits. These properties of B are robust. From a qualitative point of view, B , as a function of f_i and σ , exhibits the same properties independently of the value of the other parameters. The condition to preserve them are that $dA_i/dx_i > 0$, and $dR_i/dx_i < 0$.

Analysis of Eq. 7 for other values of p shows similar relationships between the stability of the states and their associated benefit (Figs. 3 and 4B). Fig. 4B shows the fractions of the population in shelter 1 (x_1) that maximizes the benefit B as a function of σ for 2, 3, and 4 shelters [$p = (2, 3, 4)$]. Among all potential patterns, the cockroaches adopt the same family of clustering patterns independent of the total number of shelters. The cockroaches minimize the number of occupied shelters and are equally distributed between the occupied shelters.

The mechanism favors group cohesion by avoiding dispersal among patches. Individuals optimize their partitioning according to a tradeoff between being together and access to shelter resources. This remarkable pattern of site selection corresponds to a maximum of the benefit associated with clustering balanced by limited resources.

For each value of σ , we compute the maximum benefit and the associated distributions of the individuals in the shelters. When σ increases, the maximum benefit switches from an equal partition between the shelters to all individuals grouped in only one of the equivalent shelters chosen randomly with a probability = $1/p$.

Discussion

The relationship between mechanism and optimality is an important question for group-living organism (18, 19). The collective decision-making process presented here results from a simple activation–inhibition process: the larger the population in a shelter, the lower the probability to enter and to leave the shelter. Our experimentally validated model is based on the following hypothesis: (i) individuals randomly explore the environment and encounter sites; (ii) individuals select sites according to their quality; (iii) individuals are influenced by conspecifics through social amplification, with all animals being equal; and (iv) individuals are constrained by crowding effects. Without elaborate communication, global information, and explicit comparison of available opportunities, the animals are able to assess the availability of resources and adapt the way they form groups among selected sites. The collective decision emerges from the interactions between equal individuals, initially possessing little information about their environment.

It is remarkable, then, that these rules should produce a collective pattern that maximizes individual fitness. The match among the mechanistic model (Fig. 1B), the behavioral data (Fig. 2B), and the optimality model (Fig. 4B) shows that the cockroaches can use these simple behavioral rules to make optimal decisions. Such optimization is only possible if the

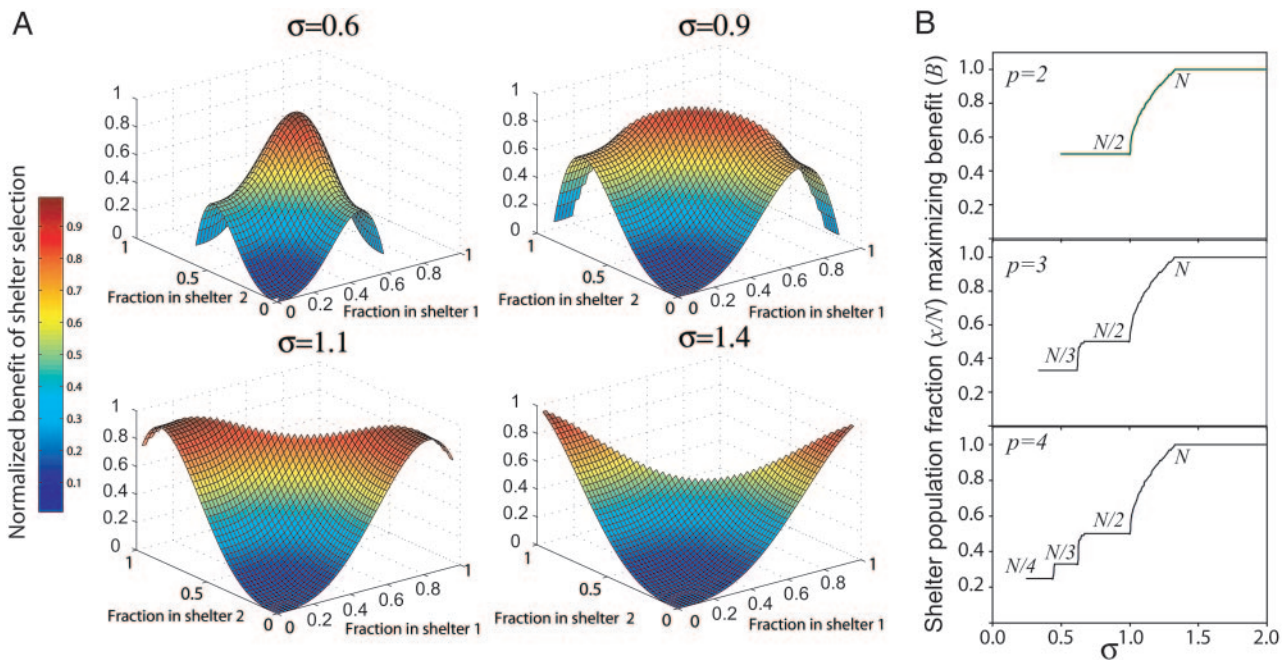


Fig. 4. ●●●. (A) Optimal benefit associated with individual distributions between two shelters of equal quality. The benefit function takes into account the advantage of forming large groups and the costs of crowding and finding the sites ($n = 2$ in Eq. 7). When $\sigma < 1$, the maximum is observed for an equal distribution of individuals between the two shelters, even when the shelters can contain more than $N/2$ individuals. As σ increases, the benefit surface spreads $\approx x_1 = x_2 = N/2$. The benefit maxima are found for all individuals in one of the shelters, thus maximizing group size. (B) Cascade of increasing benefit for two, three, and four shelters. We show the individual distribution in the shelters maximizing the benefit (Eq. 7). For a given value of σ , the benefit maximum is given by the steady-state distribution among shelters in accordance with the model for collective decision (Eqs. 3 and 4). For intermediate value of σ (≈ 0.5 , ≈ 1.25) the individuals use only some of available shelters. The dynamics induces the emergence of rational distributions of the individuals among the available shelters. These population fractions maximize group sizes, minimize the number of shelters used, and take into account crowding effects and the probability of encountering the shelter.

system remains dynamic. At any moment, on average, the individuals must be able to change their choice and leave the group to start exploring again. Otherwise, the individual repartition will tend again to a binomial distribution. Maximization of individual fitness depends on a constant flow of information.

Positive feedback based on threshold response to presence of conspecifics, described here, has already been experimentally observed in different taxa of ants, cockroaches, spiders, and vertebrates (20–24, 5). It is particularly well understood in ants, where such a mechanism leads to robustness and optimality in foraging response (25, 26). For ants, however, the aim is to maximize group-level fitness. Our study confirms that the same mechanism maximizes individual-level fitness.

We would predict that the collective decision-making process studied here should have its equivalent in many gregarious animals, including, for example, fish at aggregation devices (27). This minimal model, modulated by species traits, should be generic and relevant for understanding optimal group-size formation. Indeed, to lead to optimal group sizes, natural selection should play on only a limited number of phenotypic variations like sensitivity to crowding or interattraction among conspecifics. As is often observed with such self-organization mechanism, the biology incorporates positive feedback at the individual interaction level, and the environmental constraints produce negative feedback (28–31).

Materials and Methods

Choice tests with groups of first instar cockroach larvae (*B. germanica*) were made in Petri dishes (14 cm in diameter) with two identical small plastic caps acting as shelters (Fig. 1A). By testing equal-quality opportunities, the existence of feedback

and the role of leadership or network of interactions can be detected experimentally. When shelters differ in quality, the results can be explained by the same mechanism presented here, taking into account only a bias toward preferred shelters.

All tested cockroaches came from our reference strain. We followed the same breeding and experimental procedures as described in Amé *et al.* (13). Groups of larvae were introduced into the setup before their nocturnal activity period. We report experiments for three group sizes ($n = 20, 50$, and 100 individuals) and six shelter sizes ($S = 25, 32, 42, 68, 93, 110$ individuals). Ten combinations of N and S were tested corresponding to 10 different values of the ratio $\sigma = S/N$. For a given value of σ , between 14 and 32 tests were performed (see supporting information). The distributions of individuals among the shelters were recorded during their resting period (24 h after the beginning of the experiment) by counting the number of individuals in each shelter.

Preliminary experiments (68 tests) with two identical shelters and very large populations ($N \gg S$) were performed to estimate carrying capacity of each of the six tested shelter sizes. The fact that a large proportion of the total population remained outside the shelters until the end of the test insured that the shelters were saturated. The maximal number of individuals filling up the shelters were then counted. Based on these experiments, the functions and parameters of the model were estimated.

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