G

Gregarious Cockroaches

Michel-Olivier Laurent-Salazar[1], Sofia Bouchebti[2] and Mathieu Lihoreau[3]
[1]Faculty of Agriculture, Department of Subtropical Agro-Environmental Sciences, University of the Ryukyus, Okinawa, Japan
[2]Robert H. Smith Faculty of Agriculture, Food & Environment, Department of Entomology, B. Triwaks Bee Research Center, The Hebrew University of Jerusalem, Rehovot, Israel
[3]Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI), CNRS, University Paul Sabatier, Toulouse, France

Many of the approximately 4600 known cockroach species have been described as gregarious based on a tendency to remain in cohesive groups at various stages of their life through phenomena of mutual attraction [1]. Gregarious cockroaches are emerging models in social insect research because of the diversity of their social behavior and their phylogenetic proximity with solitary praying mantises and eusocial termites, constituting an important point of comparison with the Hymenoptera (Fig. 1) [2]. Best studied taxa are the domiciliary cockroaches, about 25 species of Ectobiidae, Blattidae, and Blaberidae species that have adapted to human habitats. These are characterized by social traits that include the sharing of a common shelter, overlapping generations of adults, non-closure of groups, equal reproductive potential of group members, an absence of task specialization, high levels of social dependence, central place foraging, social information transfer, kin recognition, and a meta-population structure [3].

Group Structure

Most cockroach species are gregarious in early stages of development. Some, such as the American cockroach (*Periplaneta americana*) and German cockroach (*Blattella germanica*), remain gregarious throughout their entire lives, while others, such as the firefly mimic cockroach (*Schultesia lampyridiformis* or *S. nitor*), only display gregarious behavior as adults. The compostion of aggregations also varies according to species. In domiciliary species (e.g., *P. americana* and *B. germanica*), aggregations are composed of all developmental stages of both males and females, while for some species, groups are typically composed of nymphs, females and one territorial male (e.g., *Gromphadorhina portentosa* and *Nauphoeta cinerea*), or no male at all (e.g., *Arenivaga grata* and *Ectobius albicinctus*). While cockroaches can sometimes form mixed-species aggregations, individuals preferentially aggregate with conspecifics and even members from the same strain or matriline when a choice is present [4]. The size of an aggregation, from a dozen to millions of individuals, depends on the amount of food resources and the carrying capacity of

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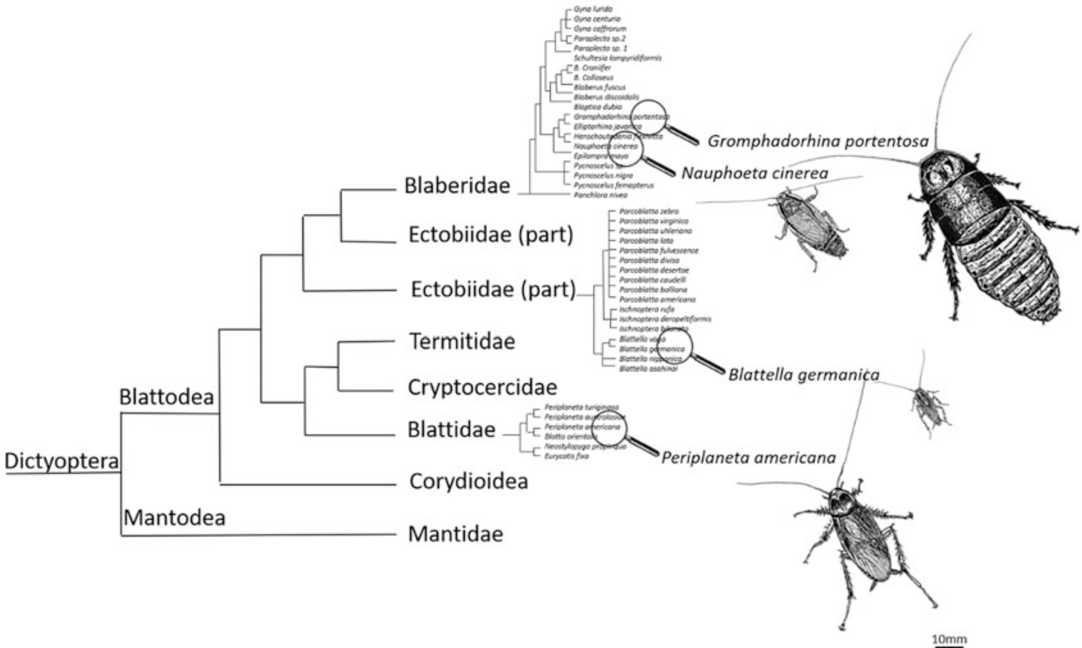


Gregarious Cockroaches, Fig. 1 Simplified phylogenetic tree of cockroach families. (Modified from Ref. [2]). The four most studied species for social behavior are highlighted with drawings

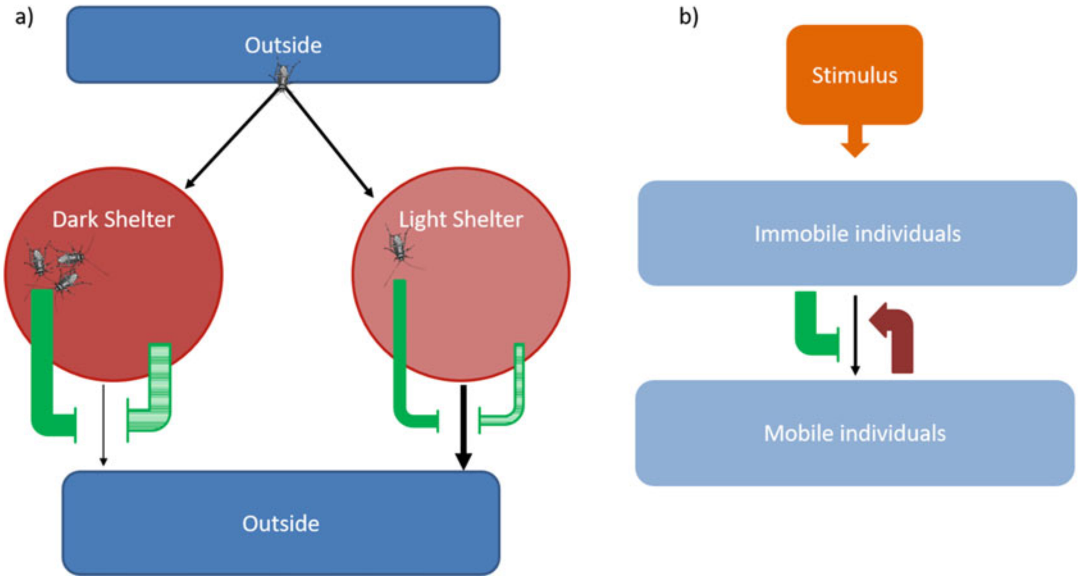
shelters available in the environment. Domiciliary and cave-dwelling species form the largest cockroach aggregations and are only found in environments where food resources are regularly renewed (e.g., bats, birds, and human wastes). Most cockroaches are nocturnal, resting in groups during the day in dark and humid shelters and foraging at night. These shelters are used repeatedly by the same groups of individuals, showing a high level of site fidelity even if the shelter has been disturbed.

Isolation Syndromes

Although naturally living in groups, most gregarious cockroaches can survive long periods of social isolation, which may explain their high success in colonizing unfavorable urban habitats [5]. Such experience can nevertheless cause physiological and behavioral disorders called "isolation syndromes." In these individuals the imaginal molt and sexual maturation are delayed, and many behaviors such as foraging, courtship, or aggregation are impaired. Social isolation experiments show that regular tactile stimulation through social contacts is key for normal development. Although the precise nature of these contacts has not yet been identified, mechanical stimulation provided by other insects (e.g., locusts) or even applied artificially (e.g., with a feather) is sufficient to accelerate the development of isolated nymphs and reproduction in adults [6]. Presumably, these tactile cues act on the corpora allata that control the production of the juvenile hormone responsible for nymphal development and sexual maturation. The more gregarious the species, the more important these developmental effects of social isolation, therefore highlighting the strong dependence of these cockroaches on their gregarious lifestyle.

Collective Behaviors

Gregarious cockroaches commonly engage in collective behaviors to locate and exploit resources in their home range (Fig. 2a). In *B. germanica* and *P.*



Gregarious Cockroaches, Fig. 2 Representation of the feedbacks involved in an (**a**) aggregation and (**b**) a collective fleeing response. Black arrows represent the probabilities of changing from one location/state to another. Green stop lines and red arrows represent negative and positive feedbacks (respectively) on the probabilities of changing place/state. Thickness of stop lines and arrows represents their relative amplitude of the probabilities. (**a**) The black arrows represent, first, the random probability of entering a shelter, regardless of its quality. The green striped stop lines represent the inhibitory effect of the quality of the shelter on a newcomer (darker shelter equals more retention). The green solid stop lines represent the inhibitory effect of conspecifics already sheltered. As the number of sheltered individuals increases, the inhibitory effect also increases, further diminishing the probability of leaving the shelter for an individual, which is shown by a thinner black arrow in the dark shelter with more cockroaches. (**b**) The fleeing event begins when a group of individuals is stimulated by an external, stressing, cue (orange arrow). The black arrow represents the probability of changing from the immobile state to the moving state. Immobile individuals have an inhibitory effect that reduces the probability of individuals to start fleeing (green stop line). This negative feedback means that individuals in larger groups have a lower probability of starting to flee than individuals in smaller groups. Fleeing individuals on the other hand have an amplifying effect on immobile individuals (red arrow). This positive feedback means that as more individuals flee (move), the probability of an immobile individual to start fleeing increases

americana, collective decisions occur during the selection of a new shelter, for instance, if the previous shelter is overcrowded or if nearby food resources are depleted. An individual's decision to settle in a new place depends on the shelter's physical properties (darkness, size, height, temperature, or hygrometry), as well as on the presence of conspecifics already resting in it as perceived by cuticular hydrocarbons passively deposited on the substrate and volatiles emitted by gut microbiota in the feces. When an exploring cockroach perceives an occupied shelter, it switches from a search mode to joining and settling. The larger the group in the shelter, the higher the probability that the newcomer joins and stays. Through this "retention effect" that resting individuals exert on newcomers, an aggregation can gradually develop, eventually leading to the selection of a unique shelter by the entire group. This behavioral model based on simple positive feedback rules has been implemented in autonomous robots that successfully reproduce the aggregation behavior observed in cockroaches and mimic their collective decision-making [7]. Similar aggregation dynamics are observed during foraging. In *B. germanica*, as in shelter selection, the selection of food sites depends on the properties of food resources (nutritional value, distance to the shelter, etc.) and the presence of conspecifics already feeding on the source.

Aggregation at food sources is based on social facilitation for feeding, so that cockroaches in large groups feed longer than those in small groups. To select a feeding site, a minimum of group size (i.e., quorum) is required. Both resting and feeding aggregations are formed and maintained by positive feedbacks [8] (Fig. 2a).

Collective decisions can also occur in response to a stress event such as the presence of predators. In this case, the aggregation suddenly disperses based on positive and negative feedbacks, resulting in collective fleeing (Fig. 2b; [9]). On the one hand, the alarm stimulus following a stress event is spread within the group by fleeing individuals, which rapidly activates individuals that have not yet started to flee. On the other hand, the number of immobile individuals (not fleeing) has an inhibitory role on the individual's probability of fleeing. The combination of these positive and negative feedbacks explains why bigger groups are slower to start fleeing, but once fleeing starts, the acceleration is greater and the group ends fleeing faster. After the disturbance, cockroaches have a strong tendency to return to their shelter. Even when their resting site is disturbed for a few consecutive days, individuals tend to return to it and only slowly start emigrating to another sheltering place.

Personalities

Cockroaches show consistent interindividual behavioral differences that have been described as personalities [10]. In *P. americana* aggregations, individuals exhibit clear differences regarding their rate of joining a shelter and their time resting within it [11]. These cockroaches also display group personality. Consistent intergroup behavioral differences have been observed in aggregations regarding the time spent outside a shelter during the active period as well as time spent inside a shelter during the inactive period. Group personality results from the interplay between individual personalities and social interactions. Social interactions can lead to amplification effects, which favor similar sheltering behaviors of individuals within a group but lead to a differentiation between groups. In turn, different group personalities regarding their time spent outside or sheltered result in different sheltering dynamics.

Kin Recognition

Cockroach aggregations are typically composed of individuals from different parental lineages. *B. germanica* uses cuticular hydrocarbons to discriminate familiar individuals according to kin classes [12]. These chemical profiles consist of a fixed number of compounds, but their relative abundances covary with genetic relatedness and are not affected by social interactions, thus providing reliable signatures for kin recognition in genetically diverse groups, where individuals interact with familiar conspecifics that do not necessarily share high levels of relatedness. Kin recognition shapes social interactions in different contexts. During mate choice, males and females reject close kin as potential mating partners, thereby enabling them to avoid fitness costs associated with inbreeding (e.g., reduced number of viable eggs). However, during the choice of a resting site, nymphs and adults preferentially interact with close kin, which may provide them indirect fitness benefits through the various advantages of group living (see below).

Population Genetics

In domiciliary species, resting aggregations are open, fluid entities in which genetically diverse individuals can transit without eliciting aggression or rejection from the residents, forming meta-populations within which individuals disperse at multiple spatial scales. Populations of *B. germanica* show clear patterns of genetic differentiation by distance based on active dispersion of individuals and isolation [13]. In this species, populations usually develop at the scale of a human dwelling from a single colonizing aggregation that gradually expands. Over time, new aggregations are established in different locations through the dispersal (e.g., adjacent rooms), settlement, and reproduction of only few individuals. These small founding populations are susceptible to genetic bottlenecking and may diverge from spatially distant aggregates through genetic drift. At larger spatial scales, however, in the absence of contiguous habitat through which active dispersal can occur (e.g. between buildings), genetic differentiation is mainly driven by human-mediated transport and is less predictable. For example, the spread of *B. germanica* across China seems to be closely connected to the development and spread of air-conditioning systems on transportation and buildings [14]. Because the rates of local population growth exceed migration fluxes at all spatial scales, members of an aggregation are expected to share relatively high relatedness levels.

Benefits of Group Living

Despite the potential costs common to all group living animals (e.g., transmission of pathogens, increased competition for resources, and increased attraction of predators), group living provides many benefits to cockroaches. First, individual cockroaches produce water vapors by respiration, and its diffusion within the group allows them to reduce water loss and better survive dry habitats. Second, cockroaches benefit from increased ambient temperature through the cumulative metabolic heat produced by the members of an aggregation, which accelerates development and sexual maturation. Third, the capacity to sense and to react to a predator is increased in an aggregation and accelerated by information transfer and swarm intelligence. Fourth, maintaining good nutrition is facilitated in a group. In addition to collective foraging allowing individuals to discover and exploit better food resources, cockroaches can feed on the wastes produced by conspecifics (e.g., exuviae, corpses, oothecal cases, feces, etc.). These food resources, often rich in proteins, are particularly important for females and nymphs. Finally, group living increases encounters between potentials mates.

Cross-References

▶ Central Place Foraging
▶ Cuticular Hydrocarbons
▶ Kin Recognition
▶ Nutrition
▶ Self-organized
▶ Termites

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