Conspecific Attraction and Shelter Selection in Gregarious Insects

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Abstract: During habitat selection, the presence of conspecifics can frequently drive a nonuniform distribution of animals across habitats of equivalent quality. In group-living species, subgroups of individuals might display mutual attraction while differing in their preferences for environmental resources. The final decision to settle requires individuals to integrate both environmental and social cues. This raises the question of the relative importance of sociality and resources preferences in determining habitat choice. In this study, we examined the interactive influence of conspecific attraction on individual resource preferences on refuge choice in groups of cockroaches. Shelters scaled to the sizes of nymphs and adult males were offered to groups of only nymphs and only males and to mixed groups. The choices of males were consistent across social conditions. Conversely, the preferences of nymphs shifted depending on the social context; the presence of males overrode the affinity nymphs had for scaled-size shelters. We developed a numerical model implementing parameters derived from these experiments to test whether the final spatial distribution of individuals originated from a differential attraction between nymphs and males that was associated with their relative body size. Finally, we propose a general framework for understanding how similar mechanisms can promote the skewed distribution of organisms at different spatial scales.

Keywords: aggregation, cockroaches, conspecific attraction, decision making, habitat selection.

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To live in fragmented environments, organisms must optimally exploit available resources. When choosing a habitat, the decision to settle is affected by the quality of the patch and the presence of conspecifics. Traditionally, models of ideal free distribution regard conspecifics as competitors that decrease the profitability of a resource. At equilibrium, individuals distribute themselves across patches to maximize their net rate of gain so that patches of different suitability can be equally profitable (Fretwell and Lucas 1970). However, the distribution of conspecifics across habitats of seemingly identical quality is frequently skewed with areas supporting high population densities, while other patches remain unoccupied (Stamps 1988). Such heterogeneous distributions result from the presence of proximate cues used by newcomers to guide their choices (Beauchamp et al. 1997; Doligez et al. 2003; Dall et al. 2005). Among these cues, attraction of newcomers to conspecifics plays a central role in habitat selection (Fletcher 2006). For instance, the probability of settling increases in the vicinity of conspecifics in territorial grasshoppers (Muller 1998), lizards (Stamps 1988, 1991), and salamanders (Quinn and Graves 1999). The formation of territorial clusters can grant direct benefits to individuals via a reduction of predation risk attributed to increased vigilance, improved defense, and dilution (Krause and Ruxton 2002). The presence of conspecifics can guide individuals toward refuges, thus reducing exposure to predators through improving refuge search efficiency (Childress and Herrnkind 2001). The presence of established residents can also provide valuable cues indicating habitat quality (Danchin et al. 1998; Donahue 2006). This strategy might be particularly relevant for inexperienced or juvenile individuals. For instance, naive house wrens show a greater attraction to conspecifics for habitat selection than individuals familiar with the environment (Muller et al. 1997). In the tube worm \textit{Galeolaria caespitosa}, larvae exhibit a gregarious response to conspecific adults fixed on the substratum (Minchinton 1997). Similarly, larvae of the coral reef fish \textit{Dascyllus} preferentially settle on corals with resident adults (Sweatman 1985; Booth 1992). The presence of residents allows habitat suitability to be directly assessed,
but it can be assessed indirectly via the detection of traces of previous activities of conspecifics. For instance, individuals preferentially select sites with residual conspecific silk in the orb-web spider *Nephila cruentata* (Schuck-Paim and Alonso 2001). Likewise, swarms of honeybees preferentially settle in nest sites containing combs (Seeley and Morse 1978). Individuals must integrate both social and environmental features to reach a decision relative to the suitability of any site. This implies that the probability of settling relies on a double modulation of individual behaviors depending on the intrinsic features of the site and the presence of conspecifics, with the final choice resulting from the interactive influence of both factors.

Within social structures, individuals might occur in subgroups that, depending on sex and ontogenetic stages, differ in their preferences for environmental features while still exhibiting mutual attraction. This raises the question of the relative importance of sociality versus resource preference in determining habitat choice. In the lobster *Panulirus argus*, EGGLESTON and LIPCIUS (1992) examined how social conditions and the scaling of lobster size to shelter dimensions regulated refuge choices of juveniles and adults. In the absence of adults, juvenile lobsters settled primarily in small shelters. This preference was shifted in the presence of adults that could fit only under large shelters. Indeed, single juveniles tended to reside with adults in large shelters rather than in sites scaled according to their body size. For single individuals, attraction toward conspecifics outweighed individual habitat preferences. However, the presence of other individuals sharing the same affinity for a resource might outweigh the attraction toward conspecifics preferring another site. Depending on the relative influence of habitat preference over interattraction, different spatial patterns can arise, from segregation between patches to the collective selection of one resource.

In this study, we examined how social interactions influence size-specific shelter choice in cockroaches. In cockroaches, previous studies investigated the dynamics of aggregation in a uniform environment (JEANSON et al. 2005) and in the presence of identical shelters (AME et al. 2004, 2006). Clustering results from positive feedback associated with the presence of conspecifics; the probability of stopping and the duration of resting time are higher as group size increases. We used the tendency of cockroaches to seek refuges within cracks to design a simplified experimental paradigm that enabled us to easily manipulate the features of refuges. We offered groups of first-instar nymphs or adult males binary choices between shelters of identical or different height. For each group, we determined their shelter preference and quantified their individual behaviors and the dynamics of aggregation. Finally, we built an agent-based model to predict how mixed groups of cockroaches would distribute when faced with different shelters. These theoretical predictions were then compared with experimental data from mixed groups.

### Material and Methods

**Study Species and Experimental Design**

*Cockroaches Blattella germanica* (L.) were collected in human dwellings in Brussels. They were reared in containers with food (dog pellets) and water ad lib. in a climate-controlled room (23°C, about 35% relative humidity, and a 13L : 11D photoperiod). In natural populations, cockroaches form mixed clusters of adults and nymphs with generation overlap. The experimental arena was 240 mm in diameter and 18 mm high and was covered with a glass plate to prevent air currents and escape of cockroaches. From the top, two vertical stands supported two shelters composed of 70-mm-diameter disks of Plexiglas (fig. A1 in the online edition of the *American Naturalist*). The height between the floor of the arena and the shelter was either 2 mm (low shelter) or 4 mm (high shelter). The outer edges of both shelters were at equal distance from the inner edge of the arena. The setup surroundings were homogenous to avoid spatial biases. The positions of low and high shelters were randomized between replicates. Sixty minutes before a trial, males (mean length 12 mm) and/or first-instar nymphs (mean length 3 mm) were collected from the same container. Immediately before the trial began, cockroaches were anesthetized with CO₂ and placed in the middle of the arena. The arena and shelters were washed with soapy water and a solution of 97% ethanol and 3% ether between trials. A webcam was coupled to a computer to record an image of the arena every second. Each replication lasted 15 h.

**Collective Behaviors**

Groups of 12 first-instar nymphs were given a choice between two low shelters (*n* = 13) or one high and one low shelter (*n* = 14). Groups of 12 males had a choice between two high shelters (*n* = 13) or one high and one low shelter (*n* = 12). Finally, mixed groups (12 nymphs and 12 males) had a choice between one high and one low shelter (*n* = 15). All cockroaches could settle in one shelter without overcrowding (fig. 1). Females were not tested in order to avoid behavioral variability due to reproductive cycle. From video recordings, the number of nymphs and/or males under each shelter was counted every 20 min for 15 h. In the presence of two identical shelters, the site gathering the most cockroaches at each time step was defined as the winning shelter. In mixed groups, we defined a collective choice as the presence of the majority of nymphs and males under the same shelter. We considered...
that segregation occurred when the majority of each group (males or nymphs) selected a different shelter. When cockroaches from one group (nymphs or males) were distributed evenly between both sites while the other group selected a shelter, it was considered that they collectively selected the site that attracted the most individuals. When the roof of the arena was removed at the end of a replication, some cockroaches were located on top of the shelters. Because we were not able to determine during video analysis whether individuals were above a shelter or not, we considered that all were below.

**Individual Behaviors**

The durations of behavioral bouts and interactions among individuals were quantified from video recordings (1 image/s). The data were used to determine three components of individual behavior.

**Spontaneous Probability per Unit of Time of Joining a Shelter.** We aimed to determine the individual probability of discovering a shelter for cockroaches moving in the arena. We measured the time spent by isolated cockroaches in the arena between two successive visits to either shelter.

**Probability of Stopping under a Shelter.** We determined the probability of stopping under a shelter by computing the proportion of moving individuals stopping spontaneously in the absence or in the presence of cockroaches. The probability of stopping under a shelter in the absence of conspecifics was calculated as the number of times an individual stopped under a shelter divided by the total number of times a cockroach visited a shelter. In the presence of cockroaches, we assessed the probability of a moving individual stopping in an aggregate under a shelter as the fraction of moving cockroaches that stopped when encountering \(N\) stopped nymphs in their vicinity (\(1 \leq N \leq 3\)). We considered cockroaches aggregated if their interindividual distance was equal or less than twice their antenna length (larva: 3 mm; male: 10 mm; see Jeanson et al. 2005).

**Probability per Unit of Time of Leaving a Shelter.** The duration of stops of nymphs and males was determined for single cockroaches and for each aggregate size (two, three, and four cockroaches) under a low and a high shelter. For each cluster size, the lifetime of an aggregate was assessed as the time when a moving individual stopped in a cluster under a shelter and the spontaneous departure of one of the aggregated cockroaches.

**Data Analysis.** Experimental data were fitted using nonlinear least squares regressions performed with SPSS (ver. 11.0, SPSS, Chicago). The parameters obtained from these regressions were subsequently implemented in the numerical model.

**Results**

**Collective Behaviors**

When nymphs had a choice between a high and a low shelter, they selected the low one (fig. 2a). Conversely, males preferentially aggregated under a high shelter (fig. 2b). In the presence of two identical shelters, groups of only nymphs and only males did not split between shelters but aggregated under one shelter (fig. 2c, 2d). This clearly indicates that nymphs and males preferred low and high
Figure 2: Experimental dynamics of site selection in cockroaches. Groups of (a) 12 nymphs (n = 14) and (b) 12 males (n = 12) facing a choice between high and low shelters; c, groups of 12 nymphs in the presence of two low shelters (n = 13), and d, groups of 12 males in the presence of two high shelters (n = 13).

Characterization of Individual Decision Rules

We determined the individual probability of discovering a shelter from experiments with pure groups of nymphs and males. Similarly, the probabilities of stopping under a shelter and leaving a shelter, depending on the size of the aggregation inhabiting it, were assessed from experiments with pure groups of nymphs and males.

Probability of Discovering a Shelter. The log-linear plots of the survival curves of the latencies spent by cockroaches in the arena suggested that the individual probability of discovering a shelter decreased with the time t between two consecutive visits of either shelter (fig. A2 in the online edition of the American Naturalist). Experimental data were then fitted with this function:

\[ \frac{dY(t)}{dt} = -\varphi \frac{Y(t)}{\lambda + t}, \]

with \( \lambda \) and \( \varphi \) as constants and where \( Y(t) \) is the fraction of individuals still exploring the arena after \( t \) seconds with \( Y(0) = 1 \). This function signifies that the probability per unit of time of discovering a shelter decreased with time.
t. The best fit for nymphs was obtained with \( \varphi = 0.96 \) and \( \lambda = 57 \) (nonlinear regression: \( F = 415.6, \text{df} = 2.62, P < .001, r^2 = 0.99 \)), and for males, it was with \( \varphi = 0.89 \) and \( \lambda = 22 \) (nonlinear regression: \( F = 203.6, \text{df} = 2.67, P < .001, r^2 = 0.98 \)).

**Probability of Stopping under a Shelter.** We determined the proportion of moving individuals that stopped under a shelter either spontaneously or after encountering one cockroach and aggregates of two and three individuals (table 1). The individual probability of stopping increases with the size of clusters. The experimental data (table 1) were fitted with the function

\[
P_{\text{stop}} = k + aX^n,
\]

where \( k, a, \) and \( X \) are constants and \( X \) is the number of cockroaches. This function means that the probability of stopping increases with the number of cockroaches in the individual’s vicinity. The constant \( k \) represents the spontaneous probability of stopping under a shelter in the absence of conspecifics (i.e., \( X = 0 \)). For nymphs, the best fit for a low shelter was obtained with \( k = 0.24, a = 0.074, \) and \( b = 0.61 \) (nonlinear regression: \( F = 1,869, \text{df} = 3.1, P < .05, r^2 = 0.98 \)), and for a high shelter, it was with \( k = 0.15, a = 0.08, \) and \( b = 0.17 \). For males, the best fit for a high shelter was obtained with \( k = 0.2, a = 0.17, \) and \( b = 0.56 \) (nonlinear regression: \( F = 5,429, \text{df} = 3.1, P < .05, r^2 = 0.99 \)), and for a low shelter, it was with \( k = 0.13, a = 0.10, \) and \( b = 0.65 \) (nonlinear regression: \( F = 4,097, \text{df} = 3.1, P < .05, r^2 = 0.99 \)).

Equation (2) governs the probability that a moving individual will stop under a shelter after it encounters \( X \) stopped individuals. However, the presence of a cluster under a shelter does not imply that a moving cockroach will encounter it. We supposed that the probability of encountering an aggregate under a shelter depends on the relative diameter of the aggregate versus the diameter of a shelter. Assuming that an aggregate of \( X \) individuals is circular, its surface \( S_X \) is given by:

\[
S_X = \pi \left( \frac{d^2}{2} \right)^2,
\]

where \( S \) is the surface of one cockroach and \( d \) is the diameter of the aggregate. Thus, \( d = (XS/\pi)^{1/2} \). Therefore, the probability of a cockroach encountering an aggregate under a shelter of diameter \( \delta \) is given by

\[
P_{\text{Encounter}} = \frac{2}{\delta} \sqrt{XS}. \quad (3)
\]

From equations (2) and (3), we obtain

\[
P_{\text{Stop}} = k + aX^n \left( \frac{2}{\delta} \sqrt{XS} \right) \quad (4)
\]

Equation (4) gives the probability that a moving cockroach stopped spontaneously under a shelter in either the absence of conspecifics (i.e., \( X = 0 \)) or the presence of conspecifics (i.e., \( X > 0 \)). For both nymphs and males, the individual probability of stopping increased with the number of conspecifics.

**Probability of Leaving a Shelter.** Log-linear plots of the survival curves of lifetimes of isolated cockroaches (\( N = 1 \)) and aggregates of different sizes (\( 2 \leq N \leq 4 \)) indicated that the probabilities of leaving a shelter decreased with the time spent stopped under a shelter (fig. A3 in the online edition of the *American Naturalist*). We proceeded in two steps to determine how aggregate size for nymphs and males affected the individual probability of leaving a shelter. First, we determined how group size affected the lifetimes of aggregates. As for the latencies spent by single cockroach in the arena, the lifetimes of aggregates increased with the time \( t \) spent aggregated (fig. A3). The experimental fraction of isolated individuals still stopped, and aggregates of size \( X \) not dissolved as a function of time \( t \) were fitted with the function

\[
\frac{dY(t)}{dt} = -\frac{\alpha}{\beta + t} Y(t), \text{ or } Y(t) = \frac{\beta^n}{(\beta + t)^n}, \quad (5)
\]

**Table 1:** Experimental proportions ± 95% confidence intervals of individuals stopping under a shelter as a function of its population \( X \)

<table>
<thead>
<tr>
<th></th>
<th>Nymphs</th>
<th></th>
<th>Males</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>X</td>
<td>Low shelter (( n ))</td>
<td>High shelter (( n ))</td>
<td>Low shelter (( n ))</td>
<td>High shelter (( n ))</td>
</tr>
<tr>
<td>0</td>
<td>.24 ± .05 (333)</td>
<td>.15 ± .04 (278)</td>
<td>.13 ± .04 (276)</td>
<td>.20 ± .06 (179)</td>
</tr>
<tr>
<td>1</td>
<td>.32 ± .06 (233)</td>
<td>.23 ± .06 (162)</td>
<td>.23 ± .06 (165)</td>
<td>.38 ± .07 (164)</td>
</tr>
<tr>
<td>2</td>
<td>.34 ± .11 (73)</td>
<td>.24 ± .10 (76)</td>
<td>.30 ± .08 (129)</td>
<td>.45 ± .09 (110)</td>
</tr>
<tr>
<td>3</td>
<td>.39 ± .10 (90)</td>
<td>...</td>
<td>.34 ± .11 (71)</td>
<td>.53 ± .15 (45)</td>
</tr>
</tbody>
</table>
where $\alpha$ and $\beta$ are constants. We determined the values of $\alpha$ for each group size of nymphs while keeping equal $\beta$ as a constraint in nonlinear regressions (table 2). We proceeded similarly for males. Equation (5) governs the lifetime of aggregates depending on their size. The next step was to assess the individual probability of leaving an aggregate. We obtained the individual probability of leaving an aggregate of $X$ cockroaches as a function of time by dividing the value of $\alpha$ by the related aggregate size (table 2). By analogy with other experimental results (De-pickère et al. 2004; Ame et al. 2004), we then fitted the individual probabilities to leave an aggregate (i.e., $\alpha/X$) with this function:

$$Q = \frac{\eta}{\theta + X^2},$$

(6)

where $\eta$ and $\theta$ are constants and $X$ is the number of cockroaches. The function $Q$ means that the probability of leaving an aggregate decreases with the number of specifics $X$. The highest probability of leaving a shelter (i.e., when an individual is alone under a site) is $\eta/(\theta + 1)$. The best fit for nymphs under a low shelter was obtained with $\eta = 2.27$ and $\theta = 0.97$ (nonlinear regression: $F = 89, df = 2.2, P < .05, r^2 = 0.97$); for nymphs under a high shelter, it was with $\eta = 94.4$ and $\theta = 9.35$ (nonlinear regression: $F = 58.12, df = 2.1, P < .1, r^2 = 0.77$). For males, the best fit under a low shelter was obtained with $\eta = 6.22$ and $\theta = 2.29$ (nonlinear regression: $F = 110, df = 2.2, P < .02, r^2 = 0.97$); under a high shelter, it was with $\eta = 2.04$ and $\theta = 0$ (nonlinear regression: $F = 634, df = 2.2, P < .01, r^2 = 0.99$).

Replacing the parameter $\alpha$ in equation (5) with equation (6) gives the individual probability of leaving a shelter as a function of its population $X$ and time $t$:

$$P_{\text{leave}} = \frac{\eta/(\theta + X^2)}{\beta + t} = \frac{\eta}{(\theta + X^2)(\beta + t)}.$$  

(7)

For both nymphs and males, the individual probability per unit of time of leaving a shelter decreased as the size of the aggregate increased.

| Table 2: Experimental probability of leaving a shelter as a function of its population $X$ |

<table>
<thead>
<tr>
<th>Nymphs</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Low shelter</strong></td>
<td><strong>High shelter</strong></td>
</tr>
<tr>
<td>$X$</td>
<td>$\alpha (n)$</td>
</tr>
<tr>
<td>1</td>
<td>1.16 (96)</td>
</tr>
<tr>
<td>2</td>
<td>.75 (37)</td>
</tr>
<tr>
<td>3</td>
<td>1.01 (15)</td>
</tr>
<tr>
<td>4</td>
<td>.55 (9)</td>
</tr>
</tbody>
</table>
were initialized outside shelters. At each time step, nymphs and males in the arena have a probability given by equation (1) to visit a shelter (equal probability of discovering shelters $i, j$). In the presence of conspecifics, the probability of stopping under a shelter depends on both the relative surface of the aggregate over the shelter area and the number of cockroaches aggregated (eq. [4]). The surfaces occupied by a larva or a male were assessed by dividing the surfaces of aggregates of nymphs or males measured from video recordings by the aggregate size. The average surface occupied by a single cockroach equaled $S_l = 25 \text{ mm}^2$ for a larva and $S_m = 210 \text{ mm}^2$ for a male. In the model, the surface of an aggregate was then determined by summing the number of nymphs and males multiplied by their respective individual surfaces ($S_l$ and $S_m$).

The probability of leaving a shelter depends on its intrinsic attractivity and population (eq. [7]). Each individual assesses the number of males and nymphs under a shelter to reach a decision. At each time step, the probabilities are updated, and the individual decision to change compartments at the next time step depends on the comparison between the calculated probabilities and a random number sampled from a uniform distribution between 0 and 1. There was no direct exchange between shelters. In simulations, the experimental timescale was preserved, and we applied time steps of 1 s/cycle. In total, 1,000 simulations were run for each condition.

**Simulation and Experimental Results for Mixed Groups of Nymphs and Males**

In mixed groups, the theoretical and experimental dynamics of aggregation were qualitatively identical. In both cases, males aggregated under the high shelter, whereas nymphs tended to occupy either site (fig. 3). To examine the proportion of experiments and simulations characterized by segregation and the selection of the low or high shelter, we determined after 15 h the number of nymphs and males under each shelter (low and high). We discarded three experiments out of 15 because less than one-third of the cockroaches aggregated under a shelter. About 50% of the experiments were characterized by the collective selection of the high shelter, and 20% of experiments ended with the choice of the low shelter (fig. 4). Segregation between males and nymphs occurred in about 30% of experiments. Representative aggregation patterns are reported in figure 1. In simulations, we explored the contribution of differential attraction among males and nymphs on shelter’s selection (fig. 4). In the absence of differential interattraction, 60% of simulations ended with a segregation between nymphs and males, and the collective selection of the low and high shelter occurred in 30% and 10%, respectively, of the simulations. The frequent segregation indicated that the affinity of cockroaches for their ideal shelters associated with the presence of conspecifics sharing the same affinity outweighed the attraction to cockroaches displaying a preference for a concurrent resource. The more frequent collective selection of the low shelter originated from the relatively larger preference of males for the low shelter than the preference of larvae for the high shelter. When differential attraction was implemented, the most frequent outcome (60%) was the selection of the high shelter. The collective choice of the low shelter and segregation occurred in 5% and 35% of simulations, respectively (fig. 4). The collective selection
of the high shelter resulted from interplay between the preference of males for the high shelter and nymphs’ attraction to males. Overall, our results suggested that the experimental aggregation patterns originated from a differential attraction between both groups of cockroaches combined with the different attractiveness of each shelter.

**Discussion**

In this study, we examined the relative importance of conspecific attraction over individual preference in determining refuge choice in groups of cockroaches. Shelters scaled to the size of nymphs and males were offered to groups of only nymphs and only males and to mixed groups. Nymph preference for refuge shifted depending on the social context. This indicates that males exerted the greatest influence in the decision of nymphs and that male presence overrode nymphs’ affinity for scaled-size shelters. Conversely, the choice of males was consistent across social conditions. A numerical model was built to test whether biased interactions between nymphs and males could account for the experimental patterns. Under the assumption that mutual attraction between nymphs and males depended on their relative body size, there was a good agreement between theoretical and observed data.

It might be argued that males may have modified the habitat preferences of nymphs by altering the structure and configuration of high shelters and that interattraction may have been of little importance in the habitat selection changes observed in mixed groups. However, several lines of evidence suggest that social factors prevailed over thigmotaxis in the dynamics of aggregation. Cockroaches preferentially cluster on folded papers previously conditioned by body contact and feces than on clean papers (Rivault and Cloarec 1998). In the presence of identical shelters, nymphs of *Blattella germanica* do not split but aggregate on one site (this study; Rivault and Cloarec 1998; Ame et al. 2004, 2006). In mixed groups of nymphs of *Periplaneta americana* and *Periplaneta fuliginosa*, the spatial segregation between shelters probably originates from interspecific differences in the cuticular hydrocarbon profiles (Leoncini and Rivault 2005; Said et al. 2005). In the absence of shelters, nymphs cluster with larger individuals, and they were only seldom found underneath late-instar individuals and adults (Ledoux 1945). Thus, we firmly believe that the attractiveness of nymphs for males relied mostly on interattraction and was only marginally under the influence of thigmotaxis.

Greater attraction toward large individuals appears to be frequent in group-living species. For instance, larvae (total length: 10–15 mm) of coral reef fish *Dascyllus albisella* are more attracted toward groups of juveniles on settlement sites (total length: 15–70 mm) than toward recruits (Booth 1992). Larger individuals can constitute more prominent visual targets to attract conspecifics (Booth 1992) or produce higher quantities of chemical
cues in relation to body size (Eggleston and Lipcius 1992). Without any explicit coding, such incident attraction to large individuals may be optimal in different ways. In cockroaches, aggregation of nymphs with adults may provide several advantages, including reduction of water loss (Yoder and Grojean 1997; Dambach and Goehlen 1999), nutrient transfer through coprophagy (Kopanic et al. 2001), and enhanced rate of development (Holbrook and Schal 1998; Holbrook et al. 2000). Naive individuals and juveniles may benefit from the proximity of adults for increased protection and more efficient foraging. For instance, large spiny lobsters use their spinose antennae to deter predators, while small individuals are mainly located within the center of clusters (Spanier and Zimmer-Faust 1988; Eggleston and Lipcius 1992). In red sea urchins, juveniles tend to aggregate with adults that offer protection against predators and improve feeding (Tegner and Dayton 1977; Breen et al. 1985; Grojean et al. 1996). In the ophiuroid Ophiothrix fragilis, the recruitment of suspended juveniles is stimulated by the presence of adults. The feeding capabilities of juveniles are enhanced by the abundance of food provided by adults, which improves larval growth and survival (Morgan and Jangoux 2004, 2005). The attraction of juveniles to adults may also contribute to reduction in physical stress. For instance, nymphs of scorpions aggregate on their mother’s back (Måhsberg 2001), and her presence increases their survival by reducing water loss (Ugoloni et al. 1986). In species with larval stages, the size of individuals correlate with age and, probably, with experience on the suitability of habitats and profitability of food patches. Thus, a differential attraction to conspecifics might represent a simple and efficient mechanism to ensure group cohesion and promote generation overlap, which characterizes natural clusters of many gregarious species, including cockroaches.

Aggregation constitutes the most widespread and simplest expression of sociality across taxa. It also represents a necessary step toward greater cooperation and influences the regulation of many collective activities in highly integrated societies (Jeanson and Deneubourg, forthcoming). Insights into the mechanisms of group formation, particularly the interactive influence of social over environmental cues, is crucial for understanding the spatial distribution of animals. We propose a general framework to understand how the interplay between conspecific attraction and environmental preference can produce a wide range of aggregation patterns and spatial organizations (fig. 5). Consider two groups of conspecifics A and B in the presence of two discrete resources (e.g., food patches, refuges) S_A and S_B. The collective exploitation of one resource requires each population to share the same interest for the patch (fig. 5: P_{A-SA} > P_{B-SA} and P_{B-SA} > P_{A-SB}) or that interattraction between groups outweighs their respective resource preferences (P_{A-SA} > P_{A-SA} and P_{B-SA} > P_{B-SB}). In contrast, segregation occurs when preferences for environmental heterogeneities prevail over mutual interattraction between populations (P_{A-SA} > P_{B-SA} and P_{B-SA} > P_{A-SB}). In this study, the collective choice of the high shelter in mixed groups relied on the invariable selection of high shelters by males (i.e., P_{A-SA} > P_{B-SA} where A = males, B = nymphs) and nymphs’ attraction to males that overrides their preference for low shelters (i.e., P_{B-SA} > P_{A-SB}). In sheep, dietary habits are formed early in life and are influenced by social factors. Scott et al. (1995) reared groups of lambs on different diets separately or together to examine how social experience and dietary habits interact to influence the exploitation of resources. Mixed groups of lambs that were reared separately on different diets segregated and essentially fed on different patches during the test. Conversely, lambs reared together with different dietary experiences often fed together (i.e., fig. 5: P_{A-SA} > P_{B-SA} and P_{B-SA} > P_{A-SB}). However, lambs reared together and made averse to one of the diets with lithium chloride fed on different patches. The administration of lithium led to dietary habits that overrode social influences (i.e., fig. 5: P_{A-SA} > P_{B-SA} and P_{B-SA} > P_{A-SA}) and induced segregation.

Individuals might be attracted by conspecifics in the absence of interference, but they can present an attenuated response or even be repelled by them under other conditions (review in Prokopy and Roitberg 2001). The advantages of grouping may decline with increasing density. The nature of social interactions may change beyond a critical threshold in population density and consequently

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**Figure 5**: Schematic illustration of the interactive influence of response to environmental heterogeneities and conspecific attraction on spatiotemporal patterning. P_A (P_B) and P_{A-SA} (P_{B-SA}) represent the intensity of interattraction among individuals of group A (B) and of group A over B (B over A), respectively. SA and SB represent two resources or spatial locations. P_{A-SA} (P_{B-SA}) and P_{B-SA} (P_{A-SA}) represent the affinity of group A (B) for resources SA (SB) and SB (SA), respectively.
alter the spatial distribution of individuals. In the red flour beetle, the aggregation at food sources is mediated by aggregation pheromones, but overcrowding triggers the production of other pheromones, causing the dispersion of individuals (Faustini and Burkholder 1987). In the barnacle Semibalanus balanoides, larvae preferentially settle in the vicinity of adult residents at low densities, but this attraction switches to bare rocks at high densities (Kent et al. 2003). In the lesser kestrels, colony attractiveness for first-year breeding birds increased with colony size, but beyond a threshold, recruits are despotically evicted by older adult residents and are obligated to join smaller colonies or to colonize new patches (Serrano et al. 2004; Serrano and Tella 2007). An increase in density can yield negative density-dependent effects such as reduced growth and increased risk of infection by pathogens that decrease the adaptive values of conspecifics (Prokopy and Roitberg 2001). In the cockroach Periplaneta americana, increasing density slows growth rate and increases mortality of nymphs, notably by cannibalism (Wharton et al. 1967).

Short-term environmental variations such as predation can also strongly influence the spatial distribution of individuals via a shift in the balance between environmental and social cues. For instance, the introduction of a predator elicited a shift in shelter preference displayed by both small and large spiny lobsters (Eggleston and Lipcius 1992). In the same way, the freshwater snails Melanoides tuberculata modified their thermal preference in the presence of conspecifics and with exposure to chemical cues from a predator (Gerald and Spezzano 2005).

Different spatial scales are also involved in nonuniform distributions of individuals, depending on sensibility to local and continuous variations in environmental cues. We can speculate that the rules underlying the nonuniform distribution across habitats can also be invoked to account for a skewed distribution of individuals within resources. Indeed, the mixed assemblages of individuals in common sites does not preclude further spatial organization. Natural refuges are not homogeneous, and individuals can distribute depending on their size in response to physical features within sites. This sorting may promote a spatial segregation within aggregates, leading to an optimal occupancy of shelters.

Similarly, the distribution of eusocial insects within nests can be skewed depending on castes or ages of workers. For instance, callow workers of the harvester ant Pogonomyrmex barbatus are located deep in the nest, whereas older individuals are mainly found close to the nest entrance (Tschinkel 1999). In P. barbatus, the profiles of particular hydrocarbons vary among workers, depending on tasks performed (Greene and Gordon 2003). Such changes in chemical signatures can influence the nature of interactions among individuals and modulate interattraction among worker castes. In addition, workers differ in their response to environmental heterogeneities. For instance, ontogenetic variations in the regulation of the foraging gene in some eusocial species parallel the transition from nest duties to foraging (Robinson et al. 2005). In particular, an upregulation of the foraging gene in the honeybee brain induces a positive phototaxis and positions workers closer to hive entrance (Ben-Shahar et al. 2003). The variability in response between worker castes to environmental cues or gradients such as humidity, luminosity, and temperature (Ceuvers 1977; Depickère et al. 2004) associated with changes in chemical profiles can affect the dynamics of aggregation and contribute to the spatial organization of individuals within nests. Thus, small behavioral differences can be amplified in a social context to influence the distribution of workers, depending on individual preferences and the nature of interattraction between worker castes. Such spatial organization can favor exchange of food and transfer of information, thereby contributing to increased efficiency in task allocation within colonies.

In conclusion, the interactive influence of environmental and social cues influences the spatiotemporal distribution of individuals. Many models (e.g., ideal free distribution, group membership games) have been developed to examine how the interplay between competition for resources and cooperation among individuals can influence the spatial distribution of animals. However, few studies addressed the question of the underlying mechanisms. The collective dynamics arising through social interactions represent an efficient source of positive feedback (Camazine et al. 2001; Jeanson and Deneubourg, forthcoming). In amplifying habitat preferences, the nonlinear responses to conspecifics could account for a more highly skewed distribution of individuals than is predicted based solely on perceived variations in habitat qualities (Muller et al. 1997; Stamps and Krishnan 2005). The identification and characterization of the individual behavioral rules underlying group formation and decision making are complementary to an approach that focuses on the economy of social life, such as aggregation economies (Giraldeau and Caraco 2000). Convergence of both approaches should prove fruitful to the understanding of the spatial distribution of organisms across heterogeneous landscapes.

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