

Stigmergy, collective actions, and animal social spacing

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Collective animal behavior studies have led the way in developing models that account for a large number of individuals, but mostly have considered situations in which alignment and attraction play a key role, such as in schooling and flocking. By quantifying how animals react to one another's presence, when interaction is via conspecific avoidance rather than alignment or attraction, we present a mechanistic insight that enables us to link individual behavior and space use patterns. As animals respond to both current and past positions of their neighbors, the assumption that the relative location of individuals is statistically and history independent is not tenable, underscoring the limitations of traditional space use studies. We move beyond that assumption by constructing a framework to analyze spatial segregation of mobile animals when neighbor proximity may elicit a retreat, and by linking conspecific encounter rate to history-dependent avoidance behavior. Our approach rests on the knowledge that animals communicate by modifying the environment in which they live, providing a method to analyze social cohesion as stigmergy, a form of mediated animal-animal interaction. By considering a population of animals that mark the terrain as they move, we predict how the spatiotemporal patterns that emerge depend on the degree of stigmergy of the interaction processes. We find in particular that nonlocal decision rules may generate a nonmonotonic dependence of the animal encounter rate as a function of the tendency to retreat from locations recently visited by other conspecifics, which has fundamental implications for epidemic disease spread and animal sociality.

movement ecology | animal space use | delayed response | territoriality | home range

Animals of the same species often are found either clustered together, e.g., in herds, or spread apart. Understanding the principles behind this heterogeneity is one of the central tenets in animal ecology with fundamental implications for population regulation, ecosystem functioning, and species evolution (1). Recent mechanistic modeling approaches (2) have produced landmark studies for the interpretation and analysis of animal spacing. Despite these fundamental advances, quantitative analyses often assume that individuals respond to one another's presence instantaneously. Although computationally advantageous, such an approach may fail to capture the nonlocality, when present, of animal interactions. One such example occurs when individuals react to one another's presence from a distance rather than only upon direct encounter. For this to occur, animals either use long-range communication, e.g., sound signals, or they acquire information about the past locations of other individuals. In the first case, the interaction is nonlocal in space, whereas in the second, the interaction is nonlocal in time. The latter is the focus of our investigation.

How nonlocal individual interactions affect the spatial distribution of sedentary, i.e., neither nomadic nor migratory, animals remains an open question. Recent studies (3, 4) advocate the need to develop a general framework to explain the broad spectrum of spacing behavior we observe: from one extreme condition, with full territorial exclusion, to an intermediate situation, with overlapping home ranges, to the other extreme, with free-ranging animals that fully share the available space. Animals that deposit marks over the terrain represent a model animal

system to develop such a framework. As individuals react to the encounter of foreign marks, they respond to the locations where other conspecifics have been in the past, making the interaction nonlocal in time. Recent studies on scent-marking animals (5–7) have taken into account nonlocal interactions, but they have investigated the formation of territorial patterns. Here, we move beyond that limitation by analyzing the collective emergence of spacing patterns resulting from animals' avoidance. We chose to focus on the endogenous mechanisms of how patterns are generated rather than asking why animals do it, which depends on the resources they aim to defend (3).

As with other collective movement phenomena, e.g., in herding (8) or schooling and flocking (9), the key to understanding the emerging dynamics is the interaction between individuals. Here, we consider the strength of the interaction as dependent on the degree of nonlocality, which we accomplish by having the probability of an individual to retreat from the encountered active foreign marks depending on how long ago the marks were deposited.

Conceptual Framework

The delayed response between mark deposition, the action of an individual, and conspecific retreat, the reaction of another conspecific, is a basic ingredient of stigmergy (10, 11), a mediated interaction mechanism whereby the changes produced endogenously in the environment by the marks of one individual elicit a response in the neighbors, which in turn respond, affecting their nearest neighbors. This cascade of events creates a feedback mechanism for the entire population, which self-organizes into a dynamic spatiotemporal pattern. Fig. 1 depicts a schematic diagram representing the feedback and interaction processes

Significance

Marking animals avoid locations recently visited by others. We conceptualized this time nonlocal avoidance behavior as stigmergy, a form of mediated interaction that gives rise to coordinated behavior from seemingly independent individuals. In so doing, the concept of stigmergy is used beyond the realm of eusocial insects. To link the population spatiotemporal patterns that emerge from the individual nonlocal rules of interaction, we construct a collective movement model whereby randomly moving animals have the tendency to avoid marks left by a conspecific, depending on the age of the mark. As a result, we are able to quantify animal decision-making processes in terms of current and past locations of other individuals, linking behavior to history-dependent actions.

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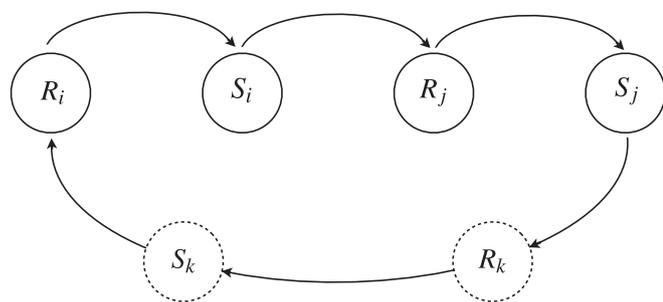


Fig. 1. Schematic representation of stigmergy in marking animals. When the animal i detects the presence of active foreign marks, it responds by retreating from the locations of the foreign marks (R_i). At the same time, the animal i itself deposits marks over the terrain, whose active set constitutes the stimulus S_i that another member j of the population detects, inducing the response R_j . In turn, animal j deposits its own marks (S_j), whose locations affect animal i again or individual k , which will react and itself produce a stimulus. The number of individuals involved in this feedback loop may be as large as the entire population or as small as just individuals i and j , depending on the locations the animals visit after their response. The dashed lines around R_k and S_k represent the fact that the number of steps necessary to affect individual i may vary because of the random nature of the movement process and, thus, of the probability of animal i encountering the stimulus (S_j).

among individuals, with animal i responding to some foreign marks initially present in the environment by producing a spatio-temporal arrangement of its own marks, the stimulus S_i . This stimulus is detected by another individual j whose reaction produces stimuli for other members of the population. Because marking is a broadcasting mechanism, the stimulus generated by individual j eventually induces a response from individual i , which in turn acts to modify the profile of its marked area, therefore creating a feedback onto the original stimulus S_i . This feedback may require two steps or a cascade of interactions via various k individuals, and thus act indirectly onto S_i .

The shrinking and growth of S_i are controlled, respectively, by the aging of the marks and the movement of the animals. The transience of the deposited cues tends to reduce the size of a marked area, because inactive marks are ignored by conspecifics. An aging mark at a given location reduces the propensity of other conspecifics to retreat from that location, which in turn increases the pressure onto individual i to move further inside its own marked area, reducing even further the spatial extent of S_i . Because a decrease in the size of S_i further reduces its spatial extent, the decay of the marks acts as a positive feedback. The other positive feedback is the movement of the animals, which helps the growth of S_i . As animals deposit marks by exploring regions beyond their inner-core areas, they increase the extent of S_i and pressure neighbors into moving away to avoid confrontation. This in turn allows them to explore even larger areas, thus further increasing the size of their marked areas. Positive feedback mechanisms act to reinforce a given process and are the key to explaining various forms of aggregation and pattern formation (see, e.g., ref. 12 for the application of reinforced random walks to represent some types of positive feedback). On the other hand, the negative feedback acts in the opposite direction of the variation of S_i whether it is a decrease or increase in its spatial extent. As marked areas get smaller, animals may traverse them quicker and thus slow their shrinking. Similarly, as marked areas get bigger, animals take longer to move across them, preventing individuals from re-marking aging marks. This results in a reduction of the growth rate of S_i .

We choose to interpret the space use of marking animals as a stigmergic interaction for three reasons. The first is that animal marking is a widespread behavior in the animal kingdom,

and although each species has evolved specialized means of communication by depositing cues on the terrain, it serves the general function of broadcasting an animal's presence. Marks contain information about identity and relative dominance (13), with many vertebrates (14) and eusocial insects (15) making use of chemical signals but also with examples in which visual marks are used, such as feathers and feces by birds. Stigmergy represents a well-developed concept that would help in studying animal space use from a general theoretical perspective, independent of the types of signals present in the marks that get deposited or the sensory modalities required for the detection of those signals. The second reason is that stigmergy makes interactive processes history dependent, which captures the fact—often neglected in quantitative analyses of animal space use—that individuals do not respond simply to the current position of other conspecifics, but also to where they have been in the recent past. A mark, when detected, represents a record of an individual's past activity in a specific location to which other conspecifics eventually respond. The third reason is that stigmergic stimulus-response association relies upon modification of the environment. As environmental heterogeneity may also affect how individuals move in space, our approach yields a method to quantify another form of spatial heterogeneity, the one generated endogenously from animal interactions. It thus may be possible to extend our current framework to provide a common currency to interpret animal space use as a function of the most important endogenous and exogenous features of the ecosystem, respectively, conspecific avoidance and environmental covariates. Promising approaches in that respect already are available and may help link population spatial distribution to animal spatial memory and landscape persistence (16), as well as to prey distribution and terrain steepness (17, 18).

In this framework of socially interacting animals, we are interested in determining how the individual movement response to the presence of conspecifics shapes the degree of segregation in the population. A useful tool to characterize the emerging spatiotemporal pattern of the population is the encounter rate of mobile animals, an instrument of broad ecological applicability (19). Most encounter estimates have relied upon basic animal movement models, in which displacement is ballistic and individuals are completely independent, which amounts to considering animals as “ideal gas” particles. This approach has been taken as a null model to estimate the frequency of meeting or associations among mobile animals (20) and has been used recently to estimate, with the help of allometric considerations in a spatially implicit context, how home range size scales with body mass (21). Here, to capture the key biological features of the movement and interaction processes that underlie animal spacing, we consider a spatially explicit scenario to determine how individual behavior affects animal space use. The focus of our analysis is the quantification of the average encounter rate, home range size, and degree of exclusivity as a function of the degree of stigmergy.

Model and Results

To study how individual-level interaction affects spacing patterns, we need to take into account the discreteness of the population and the mediated interaction events (22). We do so with an individual-based simulation in continuous time and discrete space (2D lattice) with periodic boundary conditions (see *SI Appendix* for mode details). Animals move at random among nearest-neighbor lattice sites and leave marks everywhere they go. By depositing marks, each member of the population tends to acquire space at the expense of other conspecifics. This spatial competition occurs because upon the encounter of an active foreign mark, i.e., a mark that has been deposited within a time $\tau \leq T$ in the past, an individual reacts by retreating with some probability p . The direction in which an animal retreats is the centroid of its own marked area (see *SI Appendix* to see how p

movement of the marked areas, the utilization distribution changes depending on the choice of Z : the smaller Z , the longer the time for an individual to cover its marked area relative to the time required for the marks to decay. As a result, for a given degree of stigmergy, the steepness of the utilization distribution decreases with decreasing Z . (See *SI Appendix* and *Movie S2* and *S3* to observe the dynamics of the individuals for different α and Z values.)

A quantity that may be associated directly with the amount of social cohesion is the rate of encounters among individuals. In Fig. 3, we study how the average rate R with which an individual meets conspecifics varies as a function of α for different values of Z . In Fig. 3A, for small values of α , all animals are diffusing with minimal constraint on their movement and share all the space available to them. The population in that case is “well mixed.” In this situation, the average encounter may be computed analytically through $R = 2[1 - (1 - \rho/N)^{N-1}]$ (26), which reduces to $2\rho(N-1)/N$ for small population density ρ . This limit explains why all curves in Fig. 3A converge to $R/(4D\rho) \approx 2(N-1)/N = 1.92$, where we used $N = 25$ animals and $D = 1/4$. As α increases beyond about 10^{-4} , the chance of retreating from locations recently visited by other conspecifics increases and each animal starts to be slightly confined, as shown in Fig. 3D, in which the average size of an individual’s marked area, which we may call its home range, is plotted versus α . Because the encounter rate between a random walker and a set of targets—in

this case, the other individuals of the population—is to a first approximation inversely proportional to the size of the confining domain (27), initially R increases as the size of the home range shrinks, explaining the initial increase in the encounter rate as a function of α . From Fig. 3D, it is clear that the extent and steepness of the variation of home range size as a function of α depend on the spatial competition parameter. In Fig. 3D, the normalized marked area plot, which indicates the average size of a home range relative to the size of the 2D domain, starts at increasingly higher values the larger the parameter Z for small α . This is a result of the space-filling nature of the diffusive movement, which tends to make individuals occupy larger regions of space the stronger their spatial competition. The range of reduction of home range size as a function of α also depends on the competition parameter, with larger reduction for larger Z . This explains why, in the encounter rate plot, the initial increase in R is further to the right for bigger values of Z .

Although a further increase in the degree of stigmergy reduces the size of the home ranges even more, beyond the value of α where $R/(4D\rho)$ achieves its maximum, which we call α_{\max} , the number of individuals inside a home range decreases, as shown in Fig. 3B. By comparing Fig. 3B and D, it is apparent that the number of individuals decreases more steeply than the decrease in home range size. Therefore, their ratio, the local population density, ρ_{loc} , decreases for $\alpha > \alpha_{\max}$. As the encounter rate is positively correlated to ρ_{loc} , we thus observe a decrease in $R/(4D\rho)$ for $\alpha > \alpha_{\max}$ (Fig. 3A). This is amplified further by the formation of increasingly large exclusive areas inside each home range as α increases (Fig. 3C), causing the number of possible locations where animals can encounter one another to diminish. The presence of this nonmonotonicity in the encounter rate also has been confirmed by using a flat response function, where $p(\tau)$ is constant for $0 \leq \tau \leq T$. It is an intrinsic feature of the system and a result of the interplay among the movement of the animals in partially confined spaces, the size of the confining domains, and the stigmergic interaction among the members of the population.

The value of the competition parameter also determines the relative magnitude of the fraction of the terrain used by an animal (exclusivity), shown in Fig. 3C, compared with the average size of an animal’s marked area, displayed in Fig. 3D. As explained earlier, for the same degree of stigmergy, spatial competition affects the overall size of an animal’s marked area; the stronger the competition, the larger the region each individual occupies, as clearly shown in Fig. 3D for low α values. As Z is reduced, the amount of area an animal can mark within a time T decreases, resulting in more interstitial regions and a smaller marked area. If each marked area takes up a large proportion of the total terrain, then animals are forced to have very large overlaps with their neighbors, resulting in little exclusive area, whereas smaller marked areas allow for a larger proportion of exclusivity. This causes the order of the curves in Fig. 3D to be the reverse of that in Fig. 3C.

Discussion

We have identified similarities between the mechanisms of environment-mediated interaction with which an insect colony may find resources and those with which a population of territorial animals segregate in space. In so doing, we can view animal space use processes as a decentralized coordination of tasks, a problem of utmost importance in the realm of eusocial insects as well as to the world of artificial intelligence and interactive robots in experimental biology (28). This opens the possibility of devising adaptive control procedures that are well developed in swarm intelligence studies (29), which may prove applicable to management and conservation problems. At the same time, tessellation algorithms developed from a solid quantitative understanding of animal territorial behavior might be used to improve the so-called digital hormone strategies being developed for the coordination

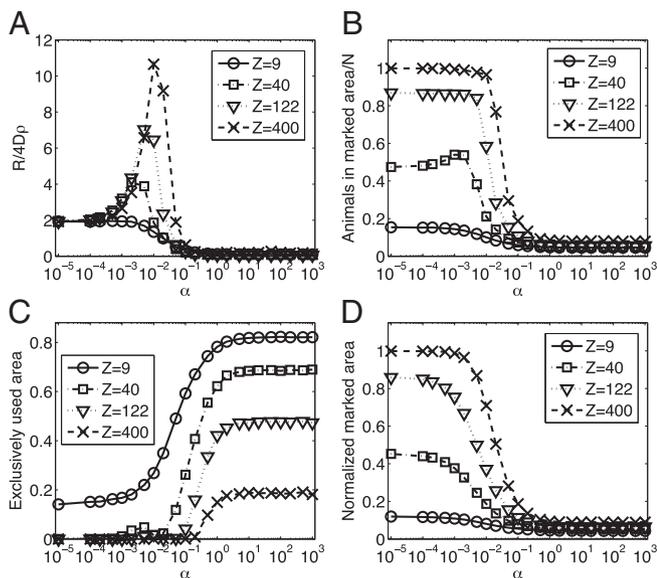


Fig. 3. Encounter rate and other demographic characteristics as a function of the degree of stigmergy. (A) Average encounter rate, (B) fraction of the average number of individuals inside a marked area, (C) fraction of the terrain used by exactly one animal, and (D) average size of a single marked area. The normalization in A is with respect to the population density and diffusion constant—more precisely, to the average diffusive rate $4D\rho$, that is, the rate for an animal to cover an area equal to the inverse of the population density ρ^{-1} . In B, we normalize the measured quantity by dividing by N , the total number of individuals in each simulation. The normalization in C and D is with respect to the size of the box (with periodic boundary conditions) that has been used in the stochastic simulations. When α is small, retreat events upon the encounter of foreign marks are reduced to a minimum, with individuals moving nearly unbounded and having no exclusive use of space, except for very low Z (C). With few constraints on their movement, an increase in Z corresponds to an increase in the diffusive area that individuals would cover, resulting in larger home ranges (D). For larger α , on the other hand, we obtain a reduction in the size of the exclusive area with increased neighbor competition, that is, with larger Z (C), without an appreciable change in home range size (D).

during which animals may be attracted by foreign marks rather than avoiding them. Future studies should try to address this aspect. Other aspects, such as the energetic expenditure to the deposition of marks, also should be taken into account. Such an approach would help reveal movement strategies that optimize the placement of cues over the terrain.

Our approach to the collective formation of spacing patterns in marking animals is relevant to many taxa among vertebrates and invertebrates and represents the first mechanistic explanation of the emergence of home ranges with areas of exclusivity and home range overlap, as conceptualized in the seminal work by William Burt 70 years ago (35). The observations of moving and interacting animals with ever-increasing resolution will provide the appropriate data to link movement data to the theory developed here. A recent study showed how to apply wavelet transform to movement trajectory data and to extract correlations between moving animal pairs (36). That approach could be extended to extract anticorrelations resulting from conspecific avoidance. Mapping the strength of the negative correlations emerging from the model animal trajectories with different degrees of stigmergy may then allow future studies to associate the degree of anticorrelation in trajectory data with the strength of the mark-avoidance response.

By associating a cost with the encounter of conspecifics, e.g., as a result of aggressive confrontations, and including foraging processes, it would be possible to study how species adapt their behavior to the distribution of resources in the environment.

This ultimately would help answer questions related to the profitability of a population's social spacing, depending on the spatiotemporal distribution of resources. The striking non-monotonicity in encounter rates we have uncovered may provide the mechanistic basis to explain the when and where of sociality vs. territorial defense (37), a classic example being the African golden-wing sunbird, which illustrates how territorial defense or sharing of flowers depends on the relative amount of nectar and the intensity of intrusions by competitors (38). Similar findings also were shown in laboratory studies in pygmy sunfish in response to changes in competition intensity (39). Our development will provide spatially explicit explanations for recent findings that relate the scaling of home range size and overlap to animal body mass (21) and help interpret allometric variability of space use across species. Finally, by considering the exchange dynamics of individuals among different social units, the neighboring marked areas, it would be possible to shed light on how the spatial extent of an epidemic outbreak is affected by the degree of spatial overlap of the individuals in a population (40).

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