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Source: Annals of the Entomological Society of America, 114(5) : 541-546

Published By: Entomological Society of America

URL: <https://doi.org/10.1093/aesa/saaa036>

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Special Collection: The Road to Sociality: Integrated Concepts of Social Behavior in Insects

Movement, Encounter Rate, and Collective Behavior in Ant Colonies

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Subject Editor: Hongmei Li-Byarlay

Received 20 July 2020; Editorial decision 11 September 2020

Abstract

Spatial patterns of movement regulate many aspects of social insect behavior, because how workers move around, and how many are there, determines how often they meet and interact. Interactions are usually olfactory; for example, in ants, by means of antennal contact in which one worker assesses the cuticular hydrocarbons of another. Encounter rates may be a simple outcome of local density: a worker experiences more encounters, the more other workers there are around it. This means that encounter rate can be used as a cue for overall density even though no individual can assess global density. Encounter rate as a cue for local density regulates many aspects of social insect behavior, including collective search, task allocation, nest choice, and traffic flow. As colonies grow older and larger, encounter rates change, which leads to changes in task allocation. Nest size affects local density and movement patterns, which influences encounter rate, so that nest size and connectivity influence colony behavior. However, encounter rate is not a simple function of local density when individuals change their movement in response to encounters, thus influencing further encounter rates. Natural selection on the regulation of collective behavior can draw on variation within and among colonies in the relation of movement patterns, encounter rate, and response to encounters.

Key words: Spatial pattern, interaction network, collective movement, collective behavior, decision-making

Distinguishing Spatial From Interaction Networks

Many aspects of social insect behavior are regulated through brief olfactory encounters (Gordon 2010), which provide cues to changes in the surrounding conditions (Gordon 2019). For example, ants use antennal contacts in which one assesses the cuticular hydrocarbons of another (Greene and Gordon 2003). Understanding encounter patterns always entails understanding spatial patterns of movement, because each individual's probability of meeting others depends on how they all move around. The paths of all of the participants create a network in space in which the encounters are the nodes and the paths between encounters are the edges. We are all familiar with managing our own movement to regulate how much space we occupy, so as to generate or avoid encounters. For example, in an elevator we move in response to each additional person that enters, to keep everyone as far apart as possible (Goffman 1976). This spatial network created by the paths of all the participants generates a different, conceptual network, in which the participants, not the encounters, are the nodes (Croft et al. 2016). This is the familiar

network of friends on Facebook, or of superspreaders who infect many others in an epidemic.

Either of these interaction networks, the one that forms in space or the conceptual network of interactions among individuals, can be considered from the perspective of individuals or as a collective pattern. For each individual, the movement of others determines its experience; which others it meets and how often it meets them, and this influences that individual's subsequent behavior. For the group, the paths of all of the participants and their encounters create a network of interactions, and this can change over time to adjust to changing conditions. For example, how foxes move around determines the changing patchwork of overlapping foraging ranges in response to changing food availability (Macdonald et al. 2015); for lions, this determines which groups hunt together (Benhamou et al. 2014).

The distinction between the individual's experience of encounters and the overall pattern of encounters became apparent to everyone in the COVID-19 pandemic. The goal of lockdowns was to change the overall pattern of movement so as to change the overall rate of encounter and thus the rate of spread of infection. From the individual perspective, each person experiences a series of encounters.

The chances of getting infected by going to a particular place depend on the movements of the other people that individual might meet. The series of encounters determine an outcome for an individual. In the aggregate, the less that everyone moves around, the less likely is an infected one to meet an uninfected one and transmit the disease. Thus how much everyone moves around and meets sets the rate of new infections for the whole population. This is a feature of the collective interaction network. It is easy to see that differences among locations in the spatial patterns of movement lead to differences in the rate of new infections. It is also clear that density, the number of people per unit area, influences the probability of encounters between infected and susceptible people.

Many theoretical models have been developed to describe the relation of spatial patterns of movement and collective patterns of encounter. The use of drift-diffusion models for animal movement, based on correlated random walks, began with studies of foraging behavior in individuals, asking how a forager's movement determines how much ground it covers and thus what it is likely to find (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Codling et al. 2008). Such models have been extended to consider how path shape affects the probability of encounter in a group. A different set of models were developed by physicists to describe interactions of particles in phase transitions (Vicsek et al. 1995, reviewed in Gorboson et al. 2016). These models have mostly been used to describe coherent movement of groups. Here the interactions generate not encounters but the avoidance of encounters, allowing a group of moving animals or cells moves together without bumping into each other. For example, a swarm of insects maintains a coherent shape while each insect keeps moving without bumping into others (Okubo 1986).

Here I outline some of the ways that spatial patterns of movement and encounter patterns are related in social insects, mostly of ants. Among social insects, the encounter patterns of ants are best studied, because ants conveniently stay on a substrate, making their movement patterns easier to track than those of taxa that fly. I will focus on our previous work. This is not a comprehensive review and there are many excellent and relevant studies not cited here.

Encounter Rate as a Cue for Density

Collective patterns of encounter depend on path shape, and also on density, the number of participants in a given area (Bartumeus et al. 2005). Because of this, individual social insects can use their experience of encounter as a cue for density, without any need to assess the collective pattern. Density can be a cue for the current state of surrounding conditions. For example, the density of scouts in a new nest site corresponds to its size (Pratt 2005); the density of ants passing on a trail corresponds to the richness of a food site (Farji-Brener et al. 2010), and so on. Because the encounter rate experienced by individuals provides feedback about surrounding conditions, the response of individuals to encounters allows the whole network to adjust to a changing environment.

Collective search, for example by ants or robots (Hecker et al. 2012), is performed by a group of individuals moving around, searching for events that could arrive and vanish at different times. For an ant colony, such events might be food; for robots searching a burning building, they could be people to be rescued. There is a tradeoff between thoroughness, searching everywhere that relevant events might be found, and extent, covering all the available area (Bartumeus et al. 2016).

Collective search depends on the relation between path shape, density, and encounter rate. In an early model of collective search

(Adler and Gordon 1992), we used a correlated random walk model as in (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Benhamou et al. 2014) to characterize movement pattern as the standard deviation of turning angle. If each searcher's path is divided somehow into steps, then there is an angle from one step to the next. A straight line has a turning angle of 0 at each step; while in a Brownian random walk, the turning angle at each step is random. The standard deviation is a measure of the variation in turning angle from step to step; for a straight line it is 0 and for a random walk it is about 5. The effectiveness of a searcher's path, in both thoroughness and extent, is associated with its standard deviation of turning angle. A Brownian random walk tends to often hover around the same place; since the searcher chooses random angles in successive steps, it turns around a lot. By contrast, a straight line is the best way to cover ground; if you want to get from here to there, the most direct way is as the crow flies.

The success of collective search, the probability of finding events scattered around the space being searched, depends both on path shape, in standard deviation of turning angle, and on the number or density of searchers. This is because the number of searchers influences the tradeoff between thoroughness and extent. If there are only a few searchers, they need to use straighter paths, further from a random walk, or they will not cover much ground and will miss most of the relevant events (Benhamou et al. 2014). But if there are many searchers, they can afford to be more thorough, each searching locally using a more random walk, because if there are enough of them, what each one misses will be found by some other searcher nearby.

The Argentine ant (Hymenoptera:Formicidae) *Linepithema humile* (Mayr) searches very effectively for resources (Human and Gordon 1999) and this helps to explain how it has invaded Mediterranean climates throughout the world (Holway et al. 2002). Argentine ants appear to manage the tradeoff between thoroughness and extent by adjusting their search paths to density (Gordon, 1995). When there are many ants searching, each ant turns around a lot, almost at random. If there are only a few ants, they walk in straighter lines. The cue to density seems to be brief antennal contacts with other ants. The apparent rule is: 'If I meet another ant often, I can turn around more. If I don't, I have to walk in a straighter line'. These simple interactions between pairs of ants function in the aggregate to adjust the scale of the network to the optimal size for the number of ants available.

We recently asked another species of ant, the pavement ant (Hymenoptera:Formicidae) *Tetramorium caespitum* (L.), to address the problem of collective search in microgravity, in the International Space Station (ISS) (Countryman et al. 2015). We sent pavement ants up to the ISS in small arenas with a barrier inside. To learn whether the ants adjust their paths when density decreased, the astronauts opened the barrier, so that the exploring ants were in a larger space, or lower density, where they met less often. The arenas were very shallow so there was not much room for the ants to float around, but every now and then an ant lost hold of the surface and went skittering around in a Michael-Jackson-like dance, until it was able to get back down. It seemed that the ants were working so hard to stay attached to the surface that they were not able to adjust their paths to search as effectively as the ants in control arenas did on Earth.

Encounter rate as a cue for density is widely used in social insects to regulate task allocation (Gordon 1996, 2010). Task allocation is linked to spatial patterns because individuals performing a particular task tend to be in the same place (Mersch 2016). This means they are likely to encounter individuals performing the same task most often (Mersch et al. 2013, Quevillon et al. 2015, Crall et al. 2018a, Ulrich et al. 2018). When they meet each other often enough,

or they finish the task (Pacala et al. 1996, Anderson and Ratnieks 1999), then ants are likely to be pushed aside to a different region, or leave to find another region, where they will encounter ants of another task, who may stimulate them to perform the new task (Gordon and Mehdiabadi 1999) or regulate their task performance (Beshers and Fewell 2001, Pinter-Wollman et al. 2012). This idea was originally called ‘foraging for work’ (Tofts and Franks 1992, Tripet and Nonacs 2004).

It is because the encounter rate depends on density that task allocation changes with colony size (Gordon 1989, Karsai and Wenzel 1998, Kang and Theraulaz 2016, Schmickl and Karsai 2018, Crall et al. 2019). As a colony grows, and numbers of workers increase, so does the probability of encounter. However, this depends on local density, number of workers nearby per unit area, not on the total number of workers in the colony.

The relation of path shape, density, and encounter rate also explains why nest shape and configuration influences the rate of encounter (Gordon 1995, Shiwakoti et al. 2014); ants move around, if they bump into a wall or obstacle and turn away, the size and shape of the space they are in affects their path shape and thus the probability that they meet. Combined with temporal patterns of activity, this can set up cycles of movement that influence interaction patterns (Cole 1990, Richardson et al. 2017). The effect of changing space constraints on encounter rate regulates nest construction (Halley et al. 2005, Gravish et al. 2013). The relation between path shape, density, and encounter rate also explains why nest connectivity affects the probability that recruiting ants will encounter others and draw them into a task (Pinter-Wollman et al. 2012, Lehue et al. 2020).

Encounter rate as a cue for density regulates nest choice in acorn ants ((Hymenoptera:Formicidae) *Temnothorax* spp.) (Pratt 2005, 2019; Gordon 2019). Scouts go out and inspect different nests. The decision to move to a new nest depends on the rate at which ants meet scouts inside a particular nest. Ants may also assess the size of an area under consideration as a new nest using encounter rate as a cue for density.

Interactions between individuals of different colonies also depend on encounter rate, which is a cue for the ants of one colony for the numbers of ants present of the other colony (Adams 1994, Greene and Gordon 2003). Ants might respond simply to the number of ants of another colony that they meet, or they could assess the rate dynamically. We asked whether rate or proportion, rather than absolute number, influences the response of ants to those of other colonies, by changing rate and number independently. We found that ants reacted to the proportion, but not to the number, of individuals of another colony that they met (Gordon et al. 1993). This indicates that ants are using the rate of encounter with ants of another colony since the rate of encounter depends on the proportion present of individuals of the other colony.

To test whether ants are responding to encounter rate, encounter rate can be manipulated experimentally. This can be done indirectly by experiments in which individuals are removed, thus changing the numbers present. Such experiments show that individuals change task when the numbers available to perform certain tasks change, because this changes the rate of encounter (Wilson 1976, Gordon 1987, Huang and Robinson 1996, Crall et al. 2018a). Workers may also respond to the amount of the task that gets done (Pacala et al. 1996, Anderson and Ratnieks 1999).

Encounter rate can be manipulated directly (e.g., Pratt 2005). In experiments with the harvester ant (Hymenoptera:Formicidae) *Pogonomyrmex barbatus* (F. Smith), we used ant mimics, glass beads coated with the extract of cuticular hydrocarbons of patrollers, to manipulate the rate of encounter between foragers and patrollers.

Harvester ant foragers leave the nest on their first trip of the day in response to the return of the patrollers, a small group of ants that go out early and encounter the patrollers of neighboring colonies. We prevented the patrollers from returning and instead introduced ant mimics at various rates. The foragers left the nest, but only when the beads were introduced at a rate of 1 per 10 s; at slower rates, the foragers were not stimulated to leave the nest. This showed that the forager’s decision to leave the nest on its first trip depends on the rate at which it meets returning patrollers (Greene and Gordon 2003, 2007).

Change in Movement in Response to Encounters

Spatial patterns of movement and interaction networks are further entwined when individuals change their movement in response to encounters. When this happens, movement patterns generate interaction networks that change movement patterns and thus change the networks. This can regulate food distribution (Depickère et al. 2008) or nest construction (Gravish et al. 2013). Adjusting movement in response to interaction produces the spectacular forms of collective movement, such as in fish schools, midge swarms, bird flocks, or migrating cells (Mayor and Theveneau 2013, Rosenthal et al. 2015, Gorboson et al. 2016). These arise because each individual adjusts its position in response to interactions with its neighbors, usually visual or tactile.

Response to infectious disease in social insects depends on encounter networks (Traniello et al. 2002, Scholl and Naug 2011, Cremer et al. 2018). The regulation of encounter rate, by changing behavior in response to encounters, allows a colony to adjust its susceptibility to infection. For example, ants that encounter infected individuals change their movements so as to reduce their exposure (Stroeymeyt et al. 2018). The spatial segregation of interactions, including the transmission of substances in trophallaxis, can function to limit the spread of disease (Quevillon et al. 2015). In bumblebees, spatial patterns of encounter influence the spread of poison (Crall et al. 2018b).

Another role of change of movement in response to interactions is to regulate traffic flow. Leaf cutter ants are likely to move away from encounters with ants in the opposite direction, thus forming lanes in each direction (Dussutour et al. 2007). Encounters between ants in opposite directions also influence where outgoing foragers go to collect leaves (Farji-Brener et al. 2010). Changes in behavior in response to encounters with nestmates, apparently mostly tactile as well as olfactory, allow army ants to build bridges across gaps in vegetation (Reid et al. 2015).

It has been difficult to study how individuals change movement in response to encounters, because most image analysis software cannot specify which ant is which after two ants have come close enough together to meet. This means the software cannot reliably track the path of a particular individual through many encounters to determine whether it changes path in response to encounters. This problem can be overcome if all of the individuals are marked (e.g., Mersch et al. 2013, Quevillon et al. 2015, Crall et al. 2018a, Ulrich et al. 2018), which works most easily in lab studies or species with small colonies. For studies with larger colonies, or studies in the field (e.g., Davidson et al. 2016), so far it has been necessary for observers to do part of the image analysis to identify which ant went which way after each encounter.

Encounter rates provide a reliable cue for density only to the extent that individuals mix at random and do not change their

movement in response to encounter. In a study of harvester ants in laboratory arenas, we considered whether certain ants were likely to seek out encounters or instead whether the encounter rate was a simple function of density. This explained individual variation in degree or number of encounters per ant. The variation among individuals was not because some ants were more gregarious, but simply because some ants were in places where local density was higher, and so they happened to engage in more encounters (Pinter-Wollman et al. 2011).

We developed a model to ask whether encounters reflect local density in harvester ant foragers inside the nest (Davidson and Gordon 2017). Encounters would not reflect local density if individuals seek out encounters, or change their movement in response to encounter so as to modify local density and influence subsequent encounter rates. The model is based on collision theory, used in particle physics to predict the probability that particles collide. We used this to establish a baseline expected rate of interaction among ants based on proximity. We tested the model using data on foragers in the entrance chamber of actively foraging harvester ant colonies in the field. We found that although ants do not mix homogeneously, trends in interaction patterns can be explained simply by the walking speed and local density of surrounding ants: foragers are not responding to encounters by changing their paths. This is similar to the results from harvester ant colonies in laboratory arenas (Pinter-Wollman et al. 2011).

The extent of variation among individuals in encounter rate, or degree distribution, is an important characteristic of the overall interaction network. It has important consequences for the spread of disease or any information using encounters. For example, in the spread of infectious disease (Bansal et al. 2007, Rosenthal et al. 2015), the extent of variability among people in the rate at which they interact with others sets the course of an epidemic. Superspreaders, people with a large number of contacts who infect many others, generate an initial high spike in infection, with a later slower spread to people who have fewer contacts or a lower degree distribution. If everyone has the same degree or number of contacts, then the epidemic would spread more linearly. In the same way, in an ant colony, if there is spread of information through encounters, then variation among individuals in degree, or number of contacts, will promote the spread of information (Pinter-Wollman et al. 2011, Campos et al. 2016, O'Shea-Wheller et al. 2017).

Individuals may differ in encounter rate without modifying their movement in response to encounters; variation among individuals in number of encounters, or degree, in an interaction network does not necessarily mean that certain individuals are seeking out or avoiding encounter. Such variation in number of encounters, or degree, is characteristic of social networks in social insects (Pinter-Wollman et al. 2011, Mersch et al., 2013, Crall et al. 2018a, Ulrich et al. 2018) and more generally in scale-free networks such as the internet (Barabási 2009).

Ants can regulate movement in response to encounters so as to regulate encounter rate itself. That is, they may avoid each other when encounter rates are too high or seek each other out when encounter rates are too low (Gordon et al. 1993). We measured encounter rate at different densities by putting the same number of ants of (Hymenoptera:Formicidae) *Lasius fuliginosus* (Latr.) in a series of arenas of increasingly large area. The larger the arena and thus the lower the density, the more ants tended to stay closer to the edge of the arena. Because the edge increased linearly while the area increased geometrically, this was a way of maintaining the highest possible density and thus the highest possible encounter rate. However,

it might also reflect a preference for edges. To test this, we observed ants at different densities on a sphere, which was a suspended soccer ball covered with a nylon stocking to give the ants a surface they could easily hold on to; these ants normally forage in trees. When density was low, the ants tended to gather together. This suggests that the ants maintain low density so as to regulate the interaction rate.

How Do Ants Assess Encounter Rate?

How do ants assess encounter rate? Calculating a rate as the number of events per unit time would require both memory of time elapsed and some way to divide intervals. Neurons use a simpler process to decide whether to fire using the rate at which they are stimulated by other neurons. The neuron acts as a 'leaky integrator': it receives electrical stimuli, each of which has a decay in electrical charge as it leaks down the neuron. If the neuron receives enough stimuli before the last has occurred, it accumulates stimulation up to a threshold, past which it is likely to fire.

We tested whether harvester ant foragers use a leaky integrator process to assess the rate of interaction with other foragers. Foragers make many trips, and in between trips they are in an entrance chamber just inside the nest entrance. Outgoing foragers leave this chamber to go out on the next foraging trip in response to the rate at which they encounter returning foragers with food (Prabhakar et al. 2012, Pinter-Wollman et al. 2013, Pless et al. 2015). We tracked the paths of outgoing and returning foragers in the excavated nest chambers of colonies actively foraging in the field. We fit the rate of encounter to a leaky integrator model and found that this explains the decisions of outgoing foragers whether to leave the nest (Davidson et al. 2016). Outgoing foragers accumulate stimuli from encounters with returning foragers with food (Greene et al. 2013) and these encounters have a decay. If available foragers do not receive enough encounters, for example when the rate of returning foragers declines, they return to the deeper nest (Pinter-Wollman et al. 2013, Pless et al. 2015).

It appears that harvester ants assess encounter rate by responding to accumulated interactions. The dynamics depend on the rate of decay in the stimulus provided by each encounter. This operates as a stochastic rather than deterministic process as in neural systems (Tkacik et al. 2010). Both the threshold at which accumulated encounters lead to a decision, and the decay rate of the stimulus produced by each encounter, may vary across individuals and colonies, as discussed below. Other species may use a similar process to assess encounter rate.

Variation Among Colonies and the Evolution of Collective Behavior

The regulation of collective behavior through interaction networks is shaped by evolution. In social insects, since colonies are the reproductive units, selection can act on variation among colonies (Gordon 2013). This suggests that we can learn about the evolution of collective behavior by examining differences among colonies in how ants respond to encounters.

One source of variation among colonies is that they can differ in the distribution of variation among individuals. That is, colony A may differ from colony B in the range of responses of individuals. Task allocation in ants is influenced by variation among individuals in response to encounter. For example, some individuals are more likely than others to respond to encounters by becoming

active or changing tasks (Charbonneau et al. 2015) (Pinter-Wollman et al. 2012). If colonies differ in the distribution of individuals that respond in a particular way, this may affect colony phenotype and ecology.

Another source of variation among colonies is colony-wide differences in response to interactions. For example, harvester ants regulate foraging in response to water stress using the response of outgoing foragers to the rate at which they engage in olfactory encounters, from antennal contact, with returning foragers. Ants lose water when out searching for food, and water is obtained by metabolizing the fats in the seeds that they eat. Thus a colony has to spend water to obtain water and food. When humidity is high, all colonies show high foraging activity. But when humidity is low, colonies differ in how they regulate this tradeoff. Some colonies are especially likely to reduce foraging activity in dry conditions. These differences among colonies seem to be heritable from mother to daughter colony. In drought conditions, natural selection is favoring the colonies that reduce foraging in dry conditions, thus sacrificing food intake so as to minimize water loss (Gordon 2013).

It seems that differences among colonies in dopamine neurophysiology influence how outgoing foragers respond to encounters with returning foragers. Colony differences in the regulation of foraging in response to dry conditions are associated with differences in the expression of genes related to dopamine (Friedman et al. 2020). A forager's response to encounters appears to depend on its hydration status (Friedman et al. 2019), apparently influenced by the humidity conditions it experienced on its previous trip (Pagliara et al. 2018). In colonies that reduce foraging more when dry, workers are more sensitive to water loss (Friedman et al. 2019) which presumably influences how much encounters with returning foragers stimulate them to leave the nest on the next trip. Ants of the colonies most sensitive to water loss are the ones that respond most, by increasing foraging activity, when administered dopamine (Friedman et al. 2018).

Variation among colonies in the relation of spatial patterns of movement and encounter rates is a starting point for investigating the evolution of collective behavior in social insects. Individual response to encounters leads to plasticity in colony response to changing conditions. Selection acts on differences among colonies in ecologically important responses. To learn how natural selection shapes collective behavior, we can investigate variation within and among colonies in the relation of movement patterns, encounter rate, and response to encounters.

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