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Trail Pheromones: An Integrative View of Their Role in Social Insect Colony Organization

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Abstract

Trail pheromones do more than simply guide social insect workers from point A to point B. Recent research has revealed additional ways in which they help to regulate colony foraging, often via positive and negative feedback processes that influence the exploitation of the different resources that a colony has knowledge of. Trail pheromones are often complementary or synergistic with other information sources, such as individual memory. Pheromone trails can be composed of two or more pheromones with different functions, and information may be embedded in the trail network geometry. These findings indicate remarkable sophistication in how trail pheromones are used to regulate colony-level behavior, and how trail pheromones are used and deployed at the individual level.

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INTRODUCTION

Ant trails are a common sight. Nevertheless, they exemplify important general biological principles: The trail networks of insect colonies are complex adaptive systems (see sidebar Insect Societies as Complex Adaptive Systems and **Figure 1**) in which the activities of many subunits, the workers, are coordinated for a common purpose, thus helping the colony. But what are the underlying mechanisms? For over 200 years (10) it has been known that foraging ants release scents—pheromones—and we now know that trail pheromones also occur in termites, stingless bees, and social wasps (11, 83, 88). Workers that find a feeding site may deposit trail pheromones when returning to the nest. The pheromones act as positive feedback, directing nestmates to the resource. This classical view of social insect pheromone trails was the inspiration for ant colony optimization (ACO; 36), a technique for obtaining computational solutions to problems that are unsolvable analytically. However, the ability of ACO to solve problems using a single simple pheromone may obscure the complexity found in real insects. Trail pheromones are used in many contexts of colony life apart from bringing workers to a food source. They are used during house hunting (e.g., 22), for recruitment to battlegrounds and escape (16, 64), or to guide the building of tunnels (110). They can be used to inform individuals about their travel direction (77, 81) or to measure the size of potential nest cavities (92). Trails may be formed of multiple pheromones with different properties (38, 79, 105), allowing colonies to form external memories or even "smell the past." Here we review research on the role of trail pheromones in the organization of insect colonies and highlight gaps in our understanding of trail pheromones.

THE CLASSICAL VIEW OF TRAIL PHEROMONES—RECRUITMENT AND WORKER ALLOCATION

The classical view of the role of trail pheromones in ant trail organization is largely based on a few experiments performed in the 1960s and 1970s (**Figure 2**). In 1962, Wilson (121) showed that

INSECT SOCIETIES AS COMPLEX ADAPTIVE SYSTEMS

What are complex systems? A complex system is a system composed of many components that interact to produce an overall collective state, structure, pattern, or outcome. Although many definitions of complex systems have been proposed, none is, and perhaps could ever be, universally accepted (89). The following are some commonly agreed on elements of a complex system:

- Modular: The system is composed of many components of relatively few types.
- Nonlinear interactions: Interactions among components often have nonlinear effects on the system; e.g., positive feedback can lead to phase transitions, hysteresis.
- Self-organized: System-level patterns generally emerge via decentralized self-organization without central control (but some central control may be present) (**Figure 1**).
- Chaotic: Outcomes cannot be exactly predicted, although general patterns can.

For example, a dune system is a complex system. Component sand grains interact with each other and the environment according to physical laws (gravity, wind resistance, friction, etc.). There is no central control to generate the patterns seen, which include features at several scales (e.g., large dunes, small ripples). The exact pattern cannot be predicted, although its general properties can. Feedback processes are important, such as a small dune causing a local reduction in wind speed, thereby causing more sand to be deposited on the lee side, in turn causing the dune to grow and migrate.

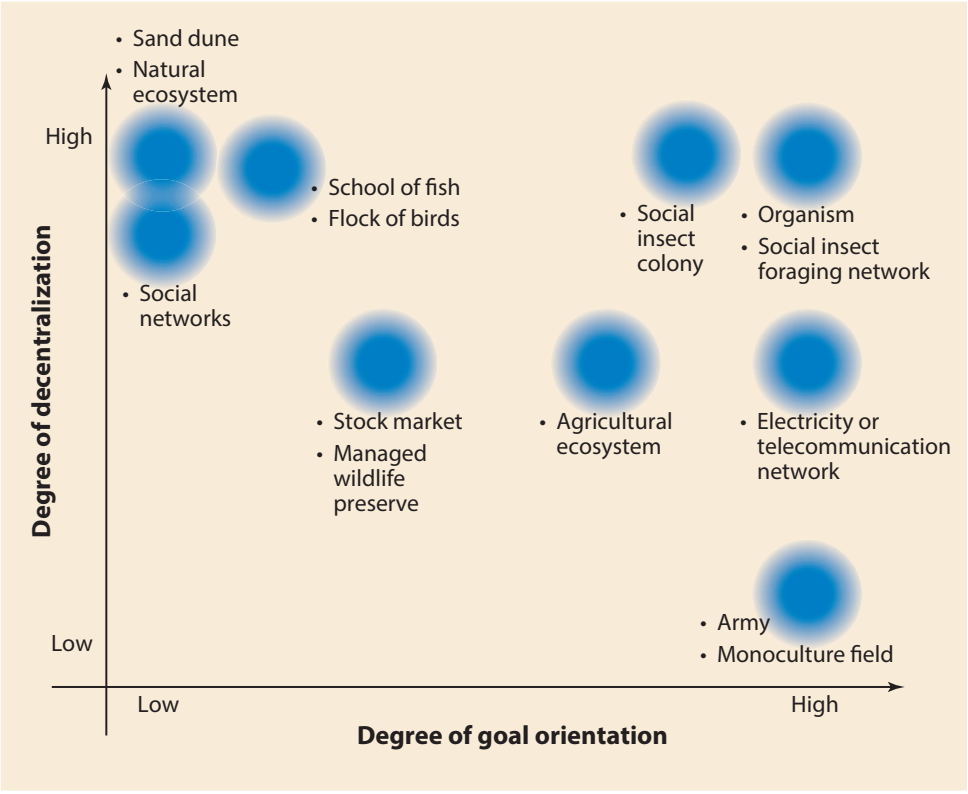

Figure 1

Examples of some complex adaptive systems in two key dimensions: degree of decentralization versus central control and goal orientation versus simple responsiveness. As the axis scales are qualitative and the exact location of each system is not known, systems are given general locations only. Human management moves ecosystems within the two-dimensional space from having no central control or overall goal (natural ecosystem, *upper left*) to having both central control and a goal (managed wildlife preserves and agricultural ecosystems, *center*; monoculture fields, *bottom right*). See sidebar Insect Societies as Complex Adaptive Systems.

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trail pheromone at the nest entrance caused *Solenopsis saevissima* workers to leave, in proportion to pheromone concentration, and then follow the trail. Hangartner (59, 60) then demonstrated that, at a trail bifurcation, the proportion of *Lasius fuliginosus* workers that select a certain branch on a bifurcation is proportional to the strength of the pheromone trail on that branch, and that more pheromone was deposited for higher-quality food sources (see also 30, 115).

These behavioral rules are simple, but their repercussions for trail organization are far-reaching. Wilson's (121) experiments demonstrated that with the simple rules "deposit trail pheromone if you have fed" and "leave the nest with a probability related to the amount of pheromone," colonies could regulate the level of recruitment to a food source and stop recruitment to overexploited or exhausted food sources (**Figure 2**). With the addition of Hangartner's (59, 60) rules "follow a trail with a probability related to the relative amount of pheromone on it" and "deposit more pheromone for better resources," a goal-directed, adaptive system arises (**Figure 1**). The implementation of these rules allows a colony to select from among multiple resources (**Figure 2**) and curb recruitment when a resource becomes overexploited.

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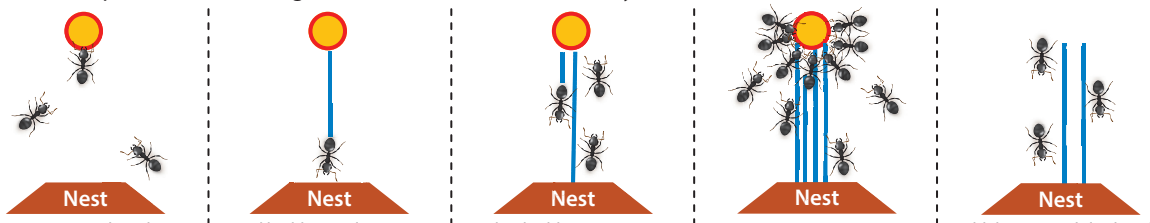
a Classical pheromone trail organization: recruitment to a newly discovered food source



Discovery: Several workers search for food outside the nest; one finds a novel food source.

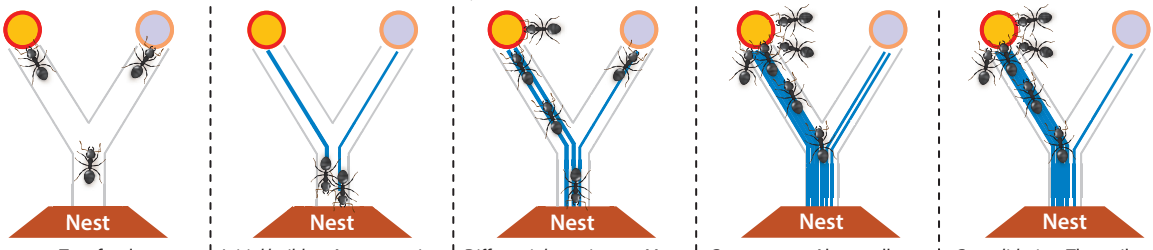
Initial buildup: Fed ant returns to nest laying trail pheromone (rule 1) causing positive feedback.

Further buildup: Recruits follow trail (rule 2), feed, and lay pheromone (rule 1), increasing positive feedback.

Saturation: Some ants unable to feed, thus do not lay pheromone (rule 1); positive feedback stabilizes.

Build down: Food depleted. No more pheromone laid (rule 1). Pheromone evaporates: negative feedback.

b Classical pheromone trail organization: colony-level choice between two food sources



Discovery: Two food sources are discovered, a good one (*left*) and a poor one (*right*).

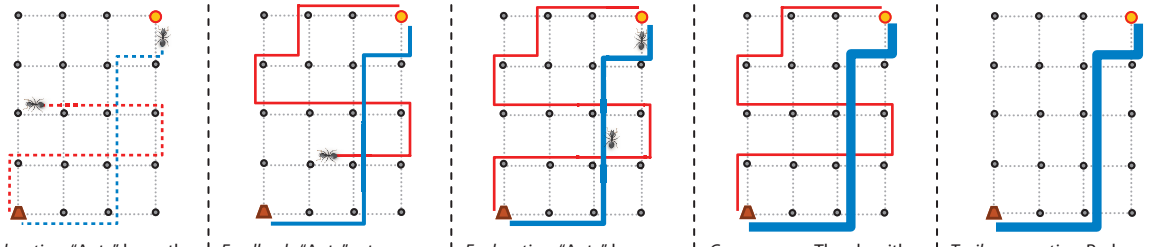
Initial buildup: Ants returning from better food source lay more pheromone (rule 1), causing positive feedback.

Differential recruitment: More ants follow stronger trail (rule 2), strengthening it further. Positive feedback.

Convergence: Almost all ants go to the good food source. The colony has chosen the good source.

Consolidation: The trail to the poor food source is not reinforced and gets weaker as it evaporates.

c Simple ant colony optimization inspired by classical pheromone trails



Exploration: "Ants" leave the nest (▲) and explore randomly until they reach the food (●).

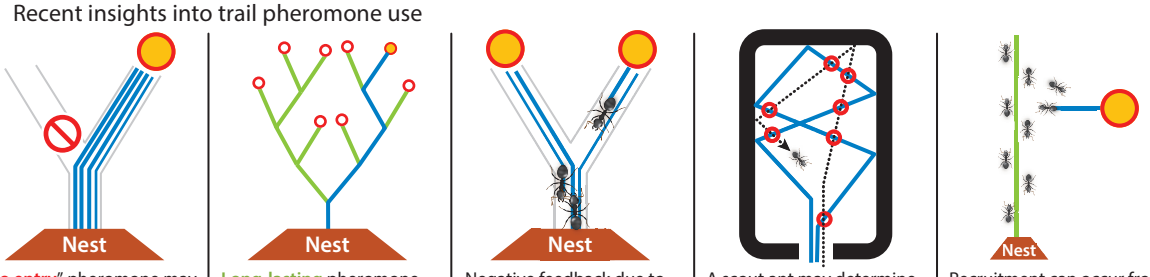
Feedback: "Ants" retrace steps, laying stronger trails on shorter routes (rule 1, positive feedback).

Exploration: "Ants" leave nest; are more likely to follow stronger trails (rule 2): positive feedback.

Convergence: The algorithm eventually converges on a short route.

Trail evaporation: Reduced influence of earlier runs prevents early convergence.

d Recent insights into trail pheromone use



"**No entry**" pheromone may help guide foragers to the rewarding branch at a trail bifurcation (99).

Long-lasting pheromone acts as an external memory to previous feeding sites, some of which can be reactivated with **short-lived** pheromone.

Negative feedback due to crowding can prevent one feeding location from dominating through the effects of positive feedback alone (24).

A scout ant may determine the size of a potential nest cavity by its intersection rate with previously laid pheromone trails (86).

Recruitment can occur from a **persistent trail**, speeding recruitment (40).

COMPLEX ADAPTIVE SYSTEMS AND COMPLEX GOAL-ORIENTED SYSTEMS

Adaptive in this context generally means able to respond to changing circumstances. Under this definition sand dunes and ecosystems (87) are complex adaptive systems (CAS). The word adaptive has a stricter evolutionary meaning, leading to confusion. There is an important difference between a system adjusting to new conditions and a system that is goal oriented. Some CAS, such as living organisms, social insect foraging networks, and electricity-distributing networks, respond to changing circumstances to achieve certain goals, such as reproduction, food intake, or uninterrupted flow. These systems respond in a goal-oriented manner. We propose the term complex goal-oriented systems (CGOS) as a useful subset of CAS. Goal orientation may arise owing to natural selection or human design. The dynamics of CGOS may be fundamentally different from those of non-goal-oriented CAS. Complex systems lie on two continua between goal oriented and simply responsive, and between decentralized and centralized control (**Figure 1**). For example, a social insect foraging network is as decentralized as a social insect colony but contains little or no conflict among individuals over reproduction, and as such it is more goal oriented.

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The interaction of these rules was demonstrated elegantly by Beckers et al. (8, 9). When simultaneously presented with alternative high- and low-quality sucrose feeders, *Lasius niger* colonies eventually send more foragers to the better feeder. This is driven by ants depositing more pheromone when returning from the better feeder. Preferentially following stronger pheromone trails also allows ants to choose shorter routes to food sources, as these routes are reinforced faster (8, 31, 50). However, *L. niger* colonies can become trapped in suboptimal foraging situations if the poor feeder is presented first, because the existing trail to the poor food source exerts such strong positive feedback that no new trail can compete with it (see also 50, 109; but see, for example, 30, 84). In contrast, *Tetramorium caespitum* is able to redirect its foragers to a newer, better food source (9). *L. niger* communicates only via trail pheromones, whereas *T. caespitum* also uses direct guiding, which allows new recruitment locations to outcompete older locations; thus *T. caespitum* has greater foraging flexibility. De Biseau et al. (30) demonstrated that other mass-recruiting ants, such as *Myrmica sabuleti*, can avoid positive-feedback traps without leader-based group recruitment, perhaps by having greater differences in recruitment strength and trail-following accuracy between high- and low-quality food sources. Errors during trail following may also allow colonies to avoid positive-feedback traps (37).

LINEAR VERSUS NONLINEAR RESPONSE TO PHEROMONES

Although the classical picture of trail pheromones was important in understanding insect colony coordination and inspired the concept of ACO (**Figure 2**; see the sidebar Complex Adaptive Systems and Complex Goal-Oriented Systems), the data underlying some basic assumptions are sparse (see Future Issues). Hangartner's studies (59, 60) were performed with artificial trails, which likely have nonnatural properties. Deneubourg's (31) choice function was derived using ant-deposited pheromone trails, and the parameters of the function have been successfully estimated in several

Figure 2

(*a*,*b*) The two classical roles of trail pheromones, (*c*) a simple ant colony optimization algorithm inspired by the classical roles, and (*d*) some examples of recent insights into trail pheromone use. Rule 1 is, "when a resource is found, return and deposit a pheromone trail with a strength related to the resource quality." Rule 2 is, "when presented with two pheromone trails, the chance of following one trail is proportional to its strength relative to the other trail." See main text for details.

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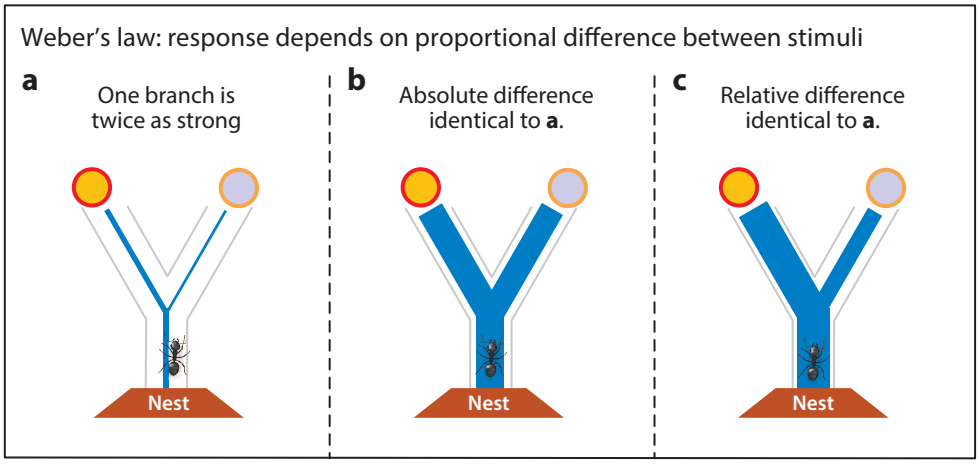

Figure 3

Weber's law and proportional processing in the detection of stimulus strength. (*a*) At low pheromone concentrations, ants are able to detect a relatively small absolute difference in the amount of pheromone on two alternative branches. In this illustration, the left branch is twice as strong (as indicated by the thickness of the *blue* lines) as the right branch. (*b*) The absolute difference between branches is the same as in panel *a*, but the proportional difference is much smaller. Weber's law states that the sensory systems of animals discriminate between stimuli based on proportional differences, rather than absolute differences (2). Hence, ants find it more difficult to discriminate between the two branches in panel *b*. (*c*) At higher stimulus intensity, ants are able to discriminate between the two branches with similar accuracy compared with the ants in panel *a* if the relative stimulus strength equals that shown in panel *a*. This is the case, because in panel *c* the left branch is twice as strong as the right branch.

species (8, 31, 117). The data suggested that the response of ants to pheromones is nonlinear in that a small difference in the amount of pheromone on two branches would cause a disproportionate number of ants to choose the stronger branch. More recently, however, two studies (97, 119) found that individuals of several ant species respond in a proportional, linear manner to trail pheromone, which is consistent with Weber's law. Weber's law states that animals compare two stimuli based on proportional differences (see **Figure 3**), rather than absolute differences, and has been confirmed in various animals across several sensory modalities (2). This suggests that Weber's law represents a common feature of many animal sensory systems, which makes it an attractive framework for interpreting ant responses to pheromones. However, Perna et al.'s (97) inability to simulate the formation of natural trail networks indicates gaps in our understanding. A fundamental but often untested assumption is that individuals respond to pheromones alone. However, alternative information sources (**Table 1**) can combine with pheromones and affect behavior. Additionally, the amount of pheromone deposited is usually unknown. It is often assumed that this is proportional to the number of individuals that have passed a particular location (e.g., 97), but the evidence for this is sparse and contradicted by other findings (see Future Issues). More research is needed to understand how absolute and relative trail strengths affect trail following (see Future Issues).

THE MANY ROLES OF TRAIL PHEROMONES IN THE ORGANIZATION OF SOCIAL INSECT COLONIES

Ants use trail pheromones to recruit nestmates to new nest sites (22, 66, 69), as do stingless bees and wasps (83). *Temnothorax albipennis* workers even use pheromone trails to assess potential nest

Table 1 Complementarity and synergy between trail pheromones and other information sources

Role for trail pheromones	Description	Other information source[a]	References
Pheromones interacting with signals and cues			
Modulation of recruitment dependent on trail usage	By sensing the amount of trail pheromone on the trail, workers can decide if more recruitment to a food source is needed. Less pheromone is laid on heavily marked trails.	Pheromone * pheromone	6, 25
External memory	Workers foraging on long-lasting food sources may deposit two trail pheromones: a long-lasting pheromone and a short-lived one. If the food source becomes unproductive, the short-lived pheromone decays rapidly, greatly reducing the number of ants visiting the depleted food source. The long-lived pheromones ensure that the food source is checked periodically and allows rapid resumption of foraging. This mechanism can also be used during nest relocation.	Long-lasting pheromone * short-lived pheromone	38, 78, 108
Recruitment to different tasks	By coupling a pheromone trail with specific physical displays, some ants can change the meaning of the pheromone trail to signal, for example, either recruitment to food, unexplored territory, or a battle.	Pheromone * physical display	62, 69, 73
Modulation of recruitment dependent on trail usage	By sensing the presence of other individuals on the trail, foragers can decide if more recruitment to a food source is needed.	Pheromone * encounter rates	26
Modulation of recruitment dependent on trail usage	By sensing the presence of home-range markings on the trail, in combination with the presence of other foragers, travel direction, and past experience, foragers can decide if more recruitment to a food source is needed.	Pheromone * home-range markings * route memory	23, 24, 35
Pheromones interacting with private information			
Local recruitment: from surrounding area to a food source	Pheromone is laid toward the nest. Scouts sensing the pheromone follow the trail away from the nest to the food source using private path-integration information to assess their location relative to the nest. Ants may also use their memory to return not to the nest, but to a nearby trunk trail.	Pheromone * memory of nest or foraging trail location	27, 43, 72
Modulation of recruitment dependent on colony satiation	Individuals may increase pheromone deposition when starved or, conversely, increase the minimum amount of food required to trigger pheromone deposition.	Pheromone * individual hunger level	90
Modulation of response to recruitment dependent on colony satiation	Workers from starved nests may decrease their response threshold to recruitment by trail pheromones and may even deposit trail pheromone themselves once recruited.	Pheromone * individual hunger level	90, 91
Reassurance to route memories	The presence of trail pheromones can allow foragers to rely more heavily on route memories, trading accuracy for speed. If an error is made foragers are informed by sensing the lack of trail pheromone.	Memory * pheromone	23, 120
Support of memory use	Trail pheromones allow greater accuracy on complex trail systems, even for experienced foragers. The benefits of route memory and trail pheromones in terms of reduced errors are additive.	Pheromone + memory	25

(*Continued*)

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Table 1 (*Continued*)

Role for trail pheromones	Description	Other information source[a]	References
Facilitate memory formation	Pheromones either constrain foragers onto a trail, ensure rapid learning of a single route, or trigger learning, possibly through a reassurance that the forager is on the correct route and hence should attempt to learn its surroundings.	Pheromone * memory	21, 25
Local recruitment: from surrounding area to a food source	Trail pheromone is dotted on the ground or emitted into the air. Foragers sensing the pheromone follow it upwind to the food source.	Pheromone * wind direction	72, 113

[a]Interactions between information sources are additive (+) or synergistic and nonlinear (*).

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sites. Workers examining a potential nest cavity lay a trail inside it on their first exploration. On their second visit, they use the number of times they cross their own pheromone trail to estimate the area of the nest site (92). Pheromone recruitment to battlegrounds occurs (16, 64) during raids on other colonies (65, 68) or to avoid competitors and partition territories (42, 63, 98). Termites, and perhaps ants, may use pheromone trails as templates around which they construct tunnels and galleries (110).

At the same time that new roles for trail pheromones are continually being discovered, the details and subtleties of the classical roles are being better understood. Trail recruitment to food sources consists of three components: (*a*) recruiting workers, thereby modulating the number of ants on the trail network, (*b*) directing recruits at bifurcations, thereby modulating which parts of a trail network are used, and (*c*) directing ants to particular locations. All three may be accomplished by the same trail pheromone (11, 59, 121), or different mechanisms may be used for recruitment and direction (ants, 12, 14; termites, 58, 107, 112; stingless bees, 88). For example, the ant *Paratrechina longicornis* deploys pheromone from the Dufour gland that causes strong attraction (recruitment) but poor trail following, whereas rectal gland pheromone causes strong trail following but poor attraction (122).

Modulation of Recruitment

Modulating recruitment to resource profitability allows colonies to allocate more foragers to profitable food sources. Many factors affect the profitability of a food source, such as sugar concentration (8, 81), energetic costs (e.g., distance) (76), and food quantity (113). Pharaoh ants, *Monomorium pharaonis*, deposit repellent trail pheromone (105), deterring ants from choosing a branch that does not lead to food.

Directing of Recruits and Modulating Trail Use

Directing workers to where they are needed is a key role of trail pheromones, but they can also have other effects. When workers are directed to a particular food source, the chances of discovering other food sources increase. If more workers are away from the nest, short-range recruitment will be more effective: The workers away from the nest can be quickly recruited to nearby food sources (see below). Constraining foragers to a set path allows the paths to be engineered to improve traffic flow by smoothing surfaces and removing obstacles (75). Confinement to a path also supports

route learning in ants (see Interaction of Pheromone Trails with Private Information/Memory) and increases the number of encounters with other ants on the trail, thus increasing information transfer on the trail (41).

Directional Information in Pheromone Trails

Although often proposed, directional information embedded in straight ant pheromone trails has never been demonstrated (18, 120). There is evidence, however, that some stingless bees lay polarized pheromone trails by increasing the amount of pheromone toward the trail end point (96). Directional information in the mucous trails laid by snails has been repeatedly documented (95), but the encoding mechanism is unknown. Additionally, the structure of the pheromone trail network itself can encode such information. On plants the trails of ants are constrained by the branching angles of the vegetation. In a wide range of ant species pheromone trail networks take on a tree-like shape, with bifurcations of about 50–60° (1, 70, 77). Pharaoh ants use the asymmetry in trail bifurcation geometry to indicate polarity: Given that the trail branches at approximately 60° when leading away from the nest, encountering a bifurcation with both paths deviating by 30° means one is heading away from the nest. When heading toward the nest one encounters one path at 30° and another at 120° (see **Figure 4**). Returning ants will then take the less-bifurcating trail (77). Indeed, ants prefer taking the less bifurcating of two paths, and this can be affected by the presence or absence of pheromone trails (44, 48).

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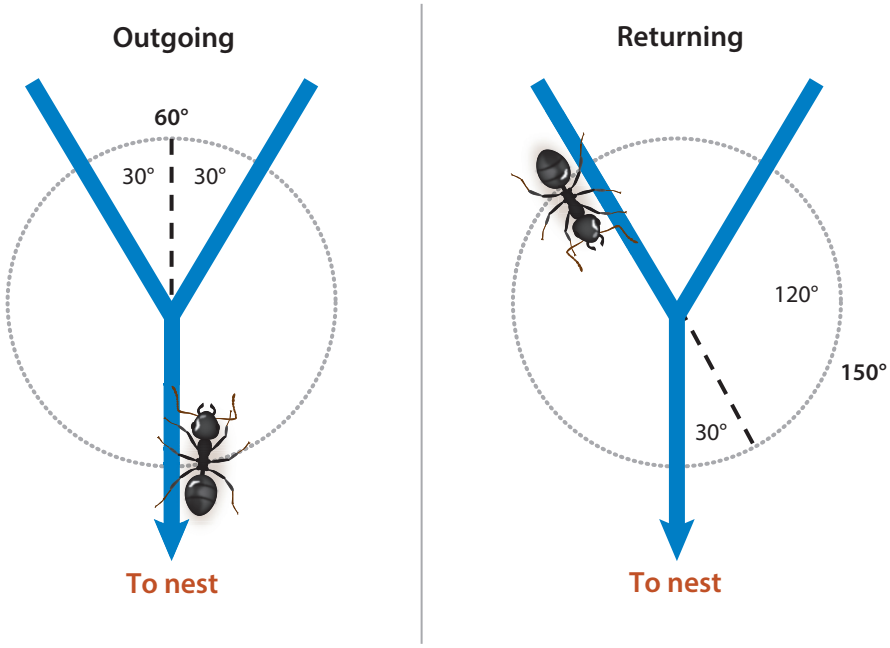

Figure 4

Trail geometry gives polarity to trail networks. Many trail networks tend to branch out from the nest at 50° to 60°. Thus, outgoing insects (*left*) must choose between turning ≈30° left or right. Conversely, when returning (*right*), they have a choice between one branch angled at ≈30° and another angled at ≈120°. This allows the ants to sense their direction of travel on a trail network.

MULTICOMPONENT TRAILS: LONG-LASTING AND SHORT-LIVED PHEROMONES

Many species use multiple trail pheromones, often from different glandular sources (see 94). The use of multiple trail pheromones is hypothesized to provide additional benefits to the foraging system (38, 79, 99, 104). Most reported multipheromone systems involve two or more attractive pheromones with different longevities (38, 107, 112, 122). Long-lasting pheromones may act as home-range markings and exploration trails, signaling that many colony members have visited the area before (31, 38, 46, 112), or as an external memory (38, 40, 78, 79); or, they may be individual-specific and ignored by nestmates (12, 92). In the termite *Reticulitermes flavipes* they can last for one year (107). Long-lasting pheromones used as home-range markings are also deposited by outgoing ants, including scouts before they discover a food source (31, 46, 107, 112). The trail laid by a scout is likely to be followed by others. Farther from the nest, home-range trails will be weaker, making it more likely that scouts will stop following a trail and begin to explore at random. This results in exploration trails fanning out, with scouts rapidly reaching the outskirts of explored territory. Thus, large areas are efficiently explored without extensive repeat exploration of marked areas (31, 46).

As workers move between their nest and a location of interest, they may deposit a long-lasting trail pheromone as well as a short-lived trail pheromone. The long-lasting pheromone may not be sensed by all workers (78), not recruit nestmates to follow the trail (93), or recruit only weakly (122). If the resource becomes exhausted, the short-term recruitment pheromone rapidly decays and the ants stop visiting the resource. If the resource becomes productive again, the trail can be reactivated by scouts depositing short-lived recruiting pheromone. The presence of the long-lived pheromone allows foraging to resume more rapidly (38, 78) and may ensure that the resource is inspected periodically. The presence of exploration pheromones also allows colonies to more rapidly adapt to changing environments, e.g., by rerouting a foraging trail after a path becomes blocked (102). This is also useful in nest relocation, where long-lived trail pheromones leading to previously reconnoitered nest sites reduce the homeless period (40, 108).

In many social insects, memory is internal but foraging on intermittent food sources is nonetheless efficient (13). By using inspector bees to recheck feeding sites, honey bee *Apis mellifera* colonies can quickly resume exploiting food sources that had previously run dry (52, 118). Why, then, do ants and termites use an external memory in the form of long-lasting trail pheromones? One advantage of an external memory may be that it is accessible to all nestmates.

Short-lived trail pheromones are not just used to guide workers to a food site. They are also often used in the short-range recruitment of foragers (27, 71, 113). Attracting foragers already in the vicinity can increase foraging range and decrease recruitment delay (27). In *Aphaenogaster cockerelli* the poison gland pheromone recruits both from the nest, in the form of a short-lived trail laid across the substrate, and locally via airborne pheromone (71). A similar situation occurs in *Lasius neoniger* (113). In *Pheidole oxyops* the short-lived trail laid from a newly discovered food item also acts as a net: Foragers intersecting the pheromone trail follow it away from the nest and toward the item (27). Short-lived pheromones are also commonly used in conjunction with long-lasting pheromones to recruit workers, which then begin following the long-lasting pheromones (16, 68, 78). Harvester ants, *Pogonomyrmex barbatus*, form long-lasting trunk trails leading from the nest. Patrollers scout the environment each morning and, if successful, return to the nest and mark the beginning of a trunk trail with a short-lived pheromone. This causes the rest of the foraging force to follow that long-lasting trunk trail along its entire length (54).

Recruitment mechanism (individual, group, or mass recruitment; 74) has often been linked to ecological niche, with some species relying on rapid food discovery and retrieval and others

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on slower recruitment and resource domination (reviewed in 114). Interspecies variation in the complexity and longevity of pheromone trails could be explained in part by differences in spatiotemporal distribution of their food resources. On the one hand, for example, the ant *L. niger*, which relies heavily on semipermanent phloem-feeding hemipteran colonies, has a pheromone trail that is quite long-lasting (45 minutes to two days) but relatively poorly followed when weak (62–70% accuracy at a bifurcation) (6, 55). The ant *Pheidole oxyops*, on the other hand, specializes in rapid retrieval of ephemeral food (dead insects); its trail pheromone is very short-lived (approximately 5 minutes), but even a trail laid by a single individual is very accurately followed (over 85% accuracy at a bifurcation) (27, 39). There is probably a trade-off between trail-following accuracy and trail longevity, as both may be a function of the pheromone volatility. The ant *P. longicornis*, which efficiently exploits both long-lived and ephemeral food sources, deploys multiple trail pheromones with different trail-following and persistence properties (29, 122). Other niches likely also require specialized pheromone trails. The trails of stingless bees, which fly, would need to be relatively volatile and emitted in great quantity to allow them to be both sufficiently durable and detectable to bees in flight. Termites foraging in covered cavities may need less-volatile pheromones used in smaller quantities (80). Despite a few examples of trail pheromones specialized to their roles, further comparative research is needed to fully understand the link between the foraging ecology of a species and the properties of its trail pheromones (see Future Issues).

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THE INTERACTION OF PHEROMONE TRAILS WITH OTHER SIGNALS AND INFORMATION SOURCES

Animals that use trail pheromones are not limited to this information. Workers use their hunger level (90, 91), individual memories (4, 55, 106), direct interactions with nestmates (49, 63), and cues inadvertently provided by nestmates (26, 33, 34) or the environment (48).

Interaction of Pheromone Trails with Private Information/Memory

When a naive forager leaves the nest, it may scout for new food sources or be guided to a known location. After a few visits it will have an accurate route memory and not need further guidance (21, 25, 55, 61, 106, 114; cf. "observe," "innovate," and "exploit" in 103). Foragers are not slaves to trail pheromones and can prioritize other information, such as memory. For example, when a pheromone trail leads in one direction but the ant remembers foraging in another direction, the ant will often choose to follow its own route memories (4, 45, 55, 61, 116), suggesting an information hierarchy (106, 116). Alternatively, foragers might follow the strategy that is likely to provide the highest payoff and switch when payoffs change (56). There is increasing evidence for flexible information-use strategies (57, 115; reviewed in 56), where individuals prioritize one information source until another is likely to be more rewarding (56).

However, when route memories and pheromone trails do not conflict, foragers can combine both information types: When a foraging *L. niger* ant is traveling to a known feeder using memory, she also uses the presence of trail pheromone to confirm her path choice. This allows the ant to walk faster and straighter (23). Thus, trail pheromones can synergize with and complement route memory, with trail pheromone acting as a reassurance. A similar situation occurs in *Atta cephalotes*: Workers turned 180° quickly reorient when replaced on a pheromone trail but walk about aimlessly if placed on an unmarked surface (120). A pheromone trail can also complement route memories, increasing trail choice accuracy of experienced *L. niger* foragers by up to 30% (25). Indeed, pheromone deposition can be increased when route memory is weak: Foragers making and subsequently correcting navigational errors increase pheromone deposition (25). *T. albipennis*

uses memories and trail pheromones in combination to note future potential nest sites. When both the memory of their local environment and their trail pheromones were intact, colonies whose nest was destroyed avoided moving to previously visited, low-quality nest sites (47). If memory was disrupted (by rearranging landmarks) or pheromone trails were removed, the ants revisited these low-quality sites. Pheromone trail use is likely flexible and context dependent, and it may be an oversimplification to state that a certain proportion of foragers will follow a trail of a certain relative strength (see Future Issues).

Trail pheromones could help improve memory formation (21): When foragers are constrained to repeatedly follow the same path, they are repeatedly exposed to the same visual panorama, which aids memorization (51). Likewise, the presence of trail pheromones might cause foragers to choose to memorize a route, as pheromone is reassurance that they are on the right path (23, 25). Supporting such a memory-improving effect is the finding that *L. niger* foragers acquire more accurate route memory when navigating a maze that is marked with pheromone (25).

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Interaction of Pheromone Trails with Other Types of Social Information

Another example of the use of multiple information sources is the use of physical (motor) displays or stridulation to enhance, or even change, the effect of a pheromone trail. Stridulation causes substrate-born vibrations and increases the attractiveness of a pheromone trail (67). In some ants, such as *Pachycondyla marginata* and *Camponotus socius*, pheromone trails are only followed if accompanied by physical displays (62, 67). The meaning of, and thus response to, a pheromone trail for *C. socius* is entirely dependent on the accompanying physical displays of the trail-laying ant. A waggle display indicates recruitment to food and causes only workers to exit the nest, whereas a jerking display signals emigration and results in workers and males exiting, with workers carrying eggs, brood, and other workers (62). Similarly, *Oecophylla longinoda* pheromone trails from the anal gland combine with different pheromonal factors and motor displays to signal either foraging, defensive, or exploration recruitment (73). Motor displays may be used to modulate pheromone-mediated recruitment depending on food quality (19).

Other information sources frequently modulate trail pheromone deposition. Home-range markings, for example, are long lasting and nonvolatile and provide cues[1] as to how often other foragers have visited a location (33, 34). Markings can take the form of cuticular hydrocarbons laid passively as foragers walk over a substrate (86), of low-volatility Dufour gland secretions from *Myrmica* ants (15), or of fecal markings from *Oecophylla* tree ants and *Messor* harvester ants, among others (53, 74). The presence of home-range markings causes *L. niger* foragers to increase pheromone deposition when returning from a food source to the nest (34). However, pheromone deposition by experienced ants decreases when the ants are returning to a food source via a trail marked by home-range markings but unmarked by trail pheromones (23). In the previous example of the effect of home-range markings, two information sources, route memories and home-range markings, interact to affect a third: trail-pheromone laying. Having two compounds that decay at different rates, such as home-range markings and trail pheromones, potentially allows ants to distinguish between areas that have been recently visited by few ants and areas that have been visited by many ants longer ago, such that the ants are effectively "smelling the past" (32). Note: What some authors consider home-range markings, others consider long-lasting trail pheromones.

[1]A signal directly conveys information and is deliberately produced for that purpose; a cue conveys information but is incidentally produced. Whether home-range markings are cues or signals is debatable, probably varies between species, and is beyond the scope of this review.

A consistent theme in the use of other information sources in combination with trail pheromones, and in the use of multiple trail pheromones, is complementarity (**Table 1**) that adds nuances and extra information, strengthens recruitment, or affects how much trail pheromone is deposited. Conversely, trail pheromones can complement other information sources, improving memory formation, increasing the reliability of route memories, or being specifically laid down when route memories are insufficient. Complementarity between information sources is widespread in biology. Examples range from cellular processes, such as apoptosis (programmed cell death), which sometimes needs both intrinsic and extrinsic signals to be triggered (3), to long-range navigation in birds, where magnetic field information may be used as a compass for orientation, but this compass is calibrated using celestial cues (20).

Is the Response to Pheromones Innate or Learned?

It is natural to assume that the ability to recognize and respond to the trail pheromone of nestmates is innate. However, recent research in stingless bees suggests that foragers learn trail pheromone identity. When reared in foster colonies of *Scaptotrigona pectoralis*, *Scaptotrigona subobscuripennis* foragers follow the pheromones of their foster colony rather than those of their mother nest, and vice versa (101). Learning the trail pheromone may allow a flexible response to changes in pheromone composition, such as those due to a new queen (100). Indeed, pheromone blends in the stingless bee *S. pectoralis* and in the ant *L. neoniger* differ between colonies, and foragers prefer to follow the pheromone of their own colony (81, 111). Jarau (81) argues that colony specificity of trail pheromones is beneficial if it helps to avoid costly intraspecific competition for food sources. Recent research on the ant *Myrmica rubra* also suggests that their response to trail pheromones may be learned (17).

FINAL REMARKS

It has been remarked that social insects are individually simple but collectively intelligent, with simple rules resulting in emergent colony behaviors (see sidebar Insect Societies and Foraging Networks as Complex Goal-Oriented Systems). However, few biologists who study individual workers would call them simple. In addition, the rules worker insects use during decision making are more numerous and nuanced than previously thought (e.g., as reviewed in 5, 85). The classical

INSECT SOCIETIES AND FORAGING NETWORKS AS COMPLEX GOAL-ORIENTED SYSTEMS

The colonies of social insects are CGOS composed of multiple organisms. Subsets of the colony, such as a foraging-trail network, can also be considered CGOS in their own right. The main components of the system are the individual workers. Coordination is largely without central control. As with individual organisms, the foraging system aims to increase survival and reproduction (of the colony), via effective foraging. Within most social insect societies there is no conflict in the foraging system. In this respect a social insect colony is different from a flock of birds or a school of fish, in which each individual forages largely for itself. Worker-worker communication is very common in the coordination of colony foraging and typically includes the deliberate transfer of information, often via trail pheromones. Social insect foraging systems are experimentally tractable. Individual workers can be tracked, added, or removed, many of the signals can be quantified, and the environment can be manipulated. The foraging systems of social insects must respond to conditions that can change rapidly, in terms of both colony needs and environmental factors, and that vary among species.

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picture of pheromone trails has taken us far in understanding the fundamental principles of collective organization and distributed decision making. However, the roles of pheromone trails are surprisingly numerous and complex and often involve the integration of multiple pheromones and other information sources. In addition, many factors, including those at individual and colony levels as well as the external environment, affect the way pheromone trails are deployed. Trail pheromones may also elicit different individual responses depending on the state of the receiver.

FUTURE ISSUES

Here we highlight four general questions about the role of trail pheromones in the organization of colony foraging that are ripe for further study.

1. How does pheromone trail strength affect trail choice? A common assumption has been that the extent to which alternative pheromone trails at a bifurcation are followed is a function of their relative strengths (8, 31, 50, 109). Although this notion is supported by theoretical analyses of branch-choice studies (31, 50), well-controlled empirical studies are rare (but see 97, 119). Most studies suffer from a lack of control for memory effects and/or a lack of information about the amount of deposited pheromone (e.g., 31, 97). The best-controlled study (60), which used artificial trails, found a linear response, in terms of ants choosing a branch, to pheromone amount. Studies using precisely controlled amounts of pheromone would be welcome and could also investigate associated factors, such as the effects of different spatial patterns of pheromone in the bifurcation area.
2. How and why do workers prioritize pheromone trails and other information sources relative to one another? When do foragers prioritize trail pheromones, when do they ignore them, and when do they use them to complement other information sources? A related subject that needs greater elucidation is the influence of the internal state of foragers (28). For example, have they been actively recruited or are they scouts? What information do they have about alternative options, and how hungry are they? Mechanistic insights should also be complemented by studies investigating how prioritization of information sources affects overall colony foraging success.
3. How are trail pheromones and pheromone trails adapted to their roles and the ecology of their species? The properties of trail pheromones vary widely in terms of volatility, chemical composition, and number of compounds. Pheromone trails may have different geometric forms, such as streaks, dots, and lines, and different widths. Some evidence suggests that volatile trails are adapted for recruitment to ephemeral prey (27, 29), but data are sparse and limited to one ecological niche, foraging on the ground. Foraging in other niches, such as underground tunnels, vegetation, or even—in the case of stingless bees—on the wing, may call for other specialized physical and chemical properties of trail pheromones. It may be instructive to consider species that do not lay pheromone trails to all food types or that lay different pheromone trails for different types of food or at different points on the trail (14, 15).
4. How do laboratory studies relate to field conditions? Great progress has been made using simplified trails in laboratory settings, such as a trail with one bifurcation leading to two feeders. As most laboratory findings are never confirmed in the field, it is difficult to know what aspects of trail pheromone organization found in the laboratory are important or even relevant in the field. Even basic observations, such as typical foraging distances and numbers of trail bifurcations of common model species, would help inform

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more appropriate laboratory studies. Other important baseline data are also worth collecting. For example, how many food sources are concurrently exploited, and do particular individual workers visit just one patch or several? How rapid and effective is recruitment to food sources at realistic distances along realistically complex paths? How often do ants make mistakes in returning home along a trail? Even small increases in the complexity of laboratory trail systems, such as having two sets of trail bifurcations in series leading to four feeder locations, yield unexpected results (25). We expect that many valuable contributions could be made by increasing studies of ant trails in the field.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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55. When trail pheromone and route memories conflict, route memory is prioritized.

60. The classical, and still perhaps best, demonstration of a linear relationship between pheromone strength and trail choice.

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