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Communication: Recruitment to Resources

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Synonyms

Odor trail; Pheromone trail; Tandem running; Waggle dance

Recruitment in social insects refers to explicit signals (as distinct from cues) that increase the number of workers at a particular place, usually leading workers to a resource. Recruitment is usually considered specific or directional, thus distinguishing it from non-specific upregulation of activity which may also result in an increase of workers at a resource. Recruitment is most common to resources such as food or nest sites, but can also take place to newly discovered territories, battle grounds, construction or excavation sites, displaced brood items, or anywhere where there is work to be done [1]. By recruiting to food, social insects can more effectively exploit resources in patchy environments, monopolize resources, and exploit an area much larger than that which a solitary insect can, or exploit food sources too large for an individual worker to handle. This effectively broadens the ecological niche of recruiting species. Recruitment to nest sites allows for cohesive and rapid colony migration.

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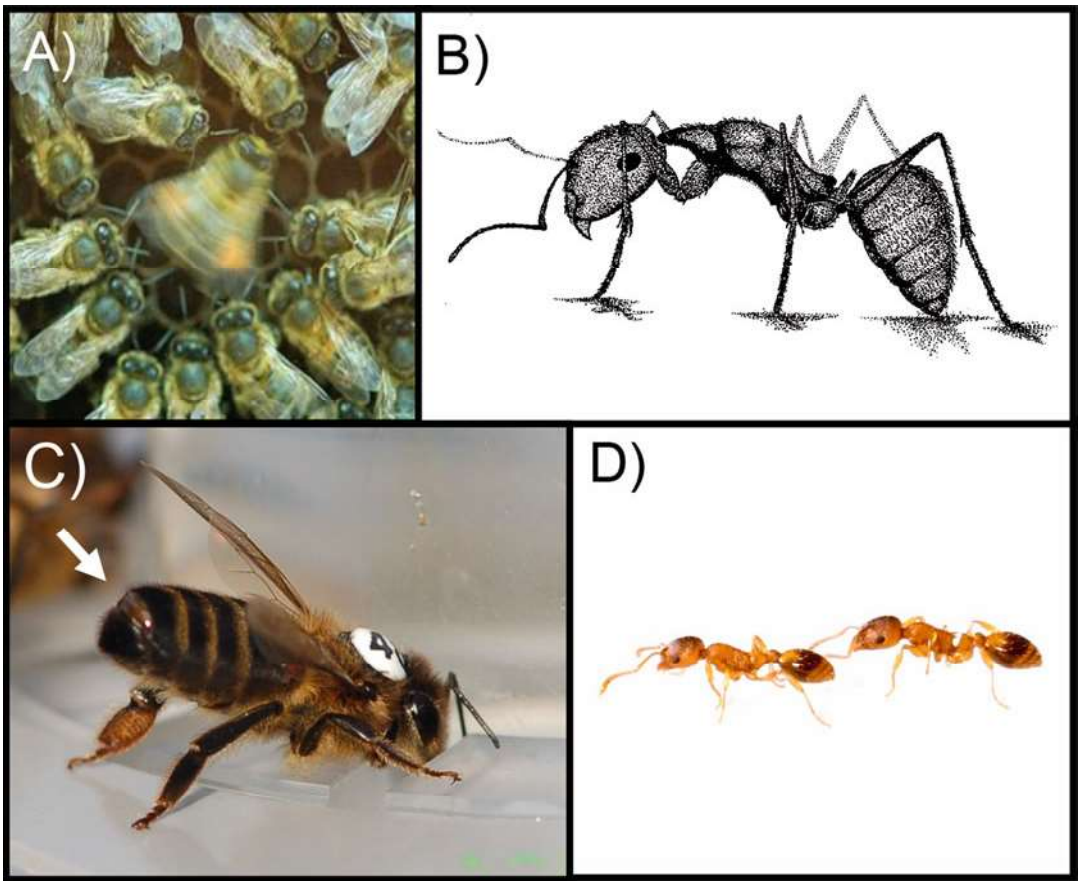
Recruitment Methods

Social insects have several methods of recruitment available to them: ▶ pheromone trails, tandem running, local recruitment, and the ▶ honey bee waggle dance. Recruitment mechanisms can be broadly divided into direct and indirect recruitment. Direct recruitment relies on the informed individual being in physical contact with the receiver. Examples include the honey bee waggle dance and tandem running. Indirect recruitment allows communication without physical contact. This includes pheromone trails and local recruitment. The type of recruitment mechanism used correlates with the size of the colony. Very small colonies may not benefit from recruitment, and species with intermediate-sized colonies may rely on individual or group level recruitment, while species with large colonies tend to use mass recruitment mechanisms. Some species may use more than one method.

Waggle Dance

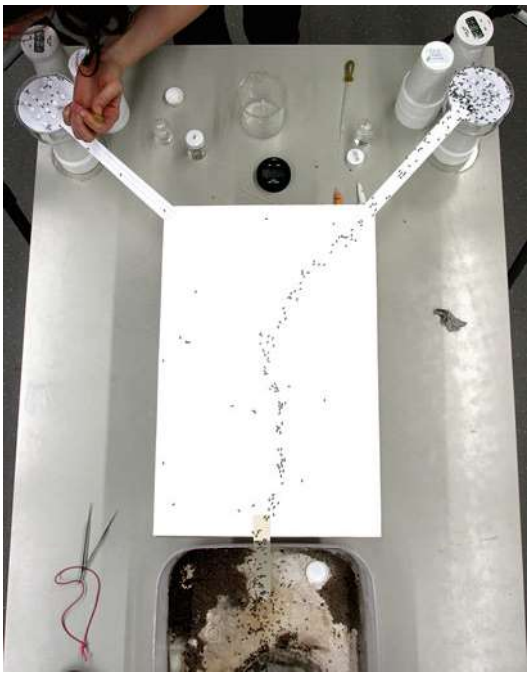
Performed exclusively by *Apis* honey bees, this unique recruitment method indicates the distance and vector of a resource relative to the colony (Fig. 1a).



Communication: Recruitment to Resources, Fig. 1 (**a**) The waggle dance. (Photo by Christoph Grüter). (**b**) A carpenter ant (*Camponotus pennsylvanicus*) depositing a pheromone trail dot. (Drawing by James F. A. Traniello [12]). (**c**) Local recruitment via calling – a western honey bee (*Apis mellifera*) releases pheromone from the Nasanov gland (indicated by the white arrow) while feeding. (Photo by Christoph Grüter). (**d**) Tandem running. An informed *Temnothorax crassispinus* worker leads a naïve recruit to a food source. (Photo by Julia Giehr)

Trail Pheromones

By depositing a line or series of dots of a volatile chemical, workers can lead other workers to a resource (Figs. 1b and 2). Pheromone trails are widely employed by ants and termites, but are also used by some ▶ stingless bee species, and have been reported in some social wasps [4]. A continuous pheromone trail results in an odor tunnel, in which the worker attempts to move using tropotaxis, comparing pheromone signal strength between the two antennae. Unlike direct recruitment methods, pheromone trail information remains in place once the signaler has left and may remain active from seconds to days depending on the volatility of the pheromone. This can result in ▶ stigmergic interactions and allow pheromone trails to act as an "external memory." Such an external memory, like the internal memory of foragers, can allow social insects to cope with a dynamic environment by allowing exhausted resources to be checked regularly and facilitate quick upregulation of recruitment if the resource becomes productive again [1]. However, as pheromone trails cannot usually be actively removed, they can have the drawback of becoming obsolete, leading foragers to locations that have recently become unproductive. In one case an explicit "no entry" signal has been reported which can counteract this. Other behaviors that can ameliorate this problem include using a



Communication: Recruitment to Resources, Fig. 2 A laboratory colony of the black garden ant *Lasius niger* making a collective decision for one food source over another. A clear pheromone trail can be seen

combination of group and mass recruitment (see below) or capping pheromone trail strength using negative feedback mechanisms.

Recruitment via trail pheromones is often divided into two broad categories: group recruitment and mass recruitment. In a mass recruitment system, a recruiting individual lays a relatively long-lasting (from minutes to days) trail from the resource to the nest, which recruits can then follow. The recruiter may continue to make repeated visits to the resource, depositing pheromone in both directions, but the recruiter's presence is not needed for successful recruitment once the trail has been deposited. The effects of mass recruitment pheromone trails are graded: the number of ants following a pheromone trail is proportional to its strength. Thus, the stronger the recruitment or the more workers recruiting, the more workers leave the nest to follow the trail. This proportionality is usually nonlinear, meaning that a doubling of pheromone trail strength more than doubles recruitment effect.

The term "group recruitment" is used in two different ways by different authors. Some use it as a special case of mass recruitment, in which the pheromone trail is so volatile that it simply triggers a single burst of recruits to leave the nest and follow the trail to the food. The high volatility prevents other ants from reinforcing the trail before it dissipates. More commonly, the term refers to a system in which a forager that has found a resource leads a group of recruits to the resource while depositing a pheromone trail. The followers remain close to the leader and follow the short-lived local trail or airborne local recruitment pheromone. Group recruitment distinguishes itself from tandem running (see below) in that the recruiter does not require feedback from the recruit in order to continue recruitment and from mass recruitment in that the presence of the recruiter is necessary for continued recruitment.

Mass recruitment requires a minimum colony size, below which trails cannot be maintained as they evaporate before they can be reinforced. This can be overcome by a combined use of group and mass recruitment.

Tandem Running

In tandem running, a recruiting individual leads one naïve individual to a specific location, usually food or a nest site (Fig. 1d) [6]. The leader walks toward the resource more slowly than she would alone, often pausing to ensure that the tandem follower is following. In some species the follower maintains almost continuous antennal contact with the leader. The tandem follower is fully reliant on the tandem leader for successful location of the resource, and it seems that followers cannot extrapolate the location of resources from prematurely terminated tandem runs. Because the leader invests time and effort in conveying information to the follower and would otherwise complete the journey faster alone, tandem recruitment has been argued to fulfill the definition of teaching [7]. It may thus be the only example of teaching in an invertebrate, although some have argued that the honey bee waggle dance is another.

A tandem running pheromone may be employed to assist the follower. This has been argued to be the evolutionary precursor of trail pheromone recruitment [10], and the distinction between tandem running and group recruitment can be unclear. As a working definition, tandem running can be considered one-to-one leading of a recruit by a recruiter, with feedback from the recruit. In group recruitment one ant leads a group of one or more ants, and the recruiter (but not the recruit) is critical to continued recruitment. In mass recruitment, the immediate presence of the recruiter is not required. In reality, tandem running, group recruitment, and mass recruitment may not be well-defined categories but rather points on a continuum.

Tandem Carrying

Workers may pick up and carry naïve individuals to a resource [9]. Carried individuals could conceivably use path integration to deduce their location at the resource [11]. Little is known about this relatively rare and poorly studied form of recruitment.

Local Recruitment

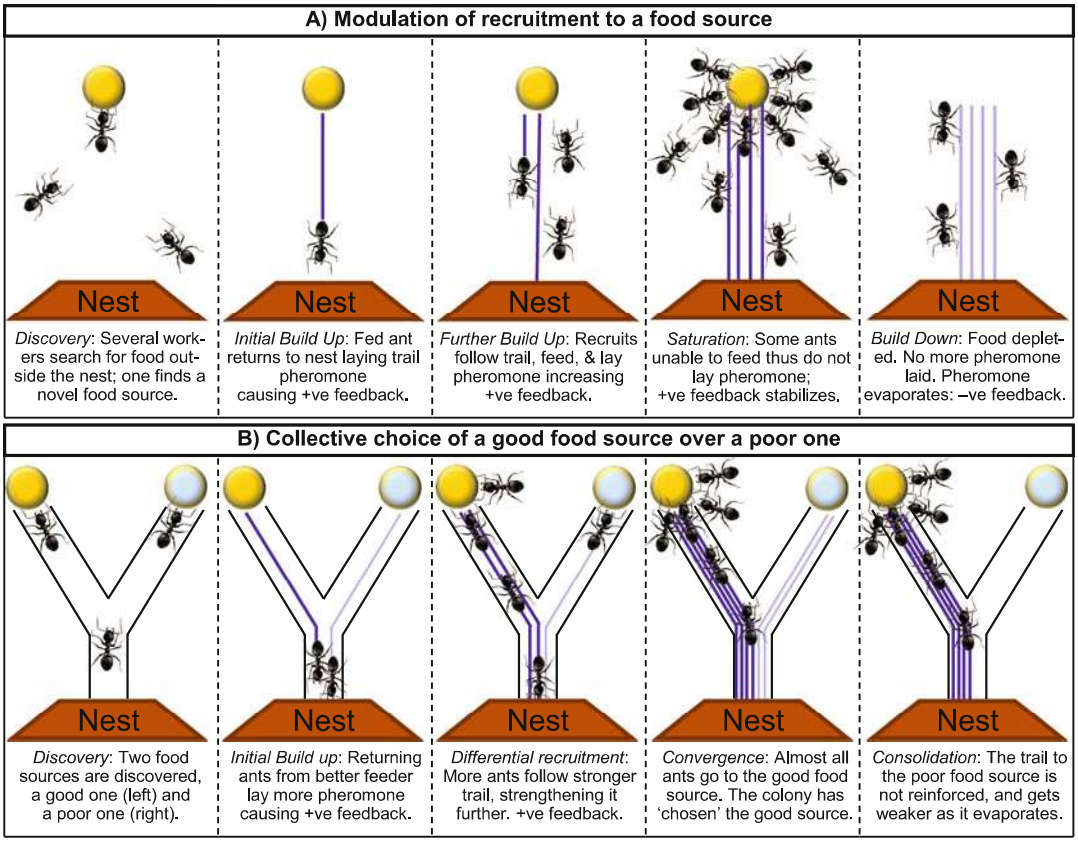
A recruiter may emit a local signal – usually a volatile pheromone (Fig. 1c) – but occasionally also a ▶ vibration or stridulatory signal, which acts to lead workers to the vicinity to the resource. Workers follow the pheromone strength gradient via osmotropotaxis or increase searching in the local area (kinesis), or they may follow the signal upwind. Honey bees (*Apis mellifera*) use local recruitment via the Nasanov pheromone to call nestmates toward the hive entrance or a potential nest site, as well as to profitable food sources (Fig. 1c). Pheromone trails from a resource to the nest may also act as a local recruitment signal by acting as a net, catching workers that cross the trail and channeling them to the resource. Workers meeting a trail outside the nest can follow it outward, as they can use path integration or other navigational abilities to deduce the location of the nest [3]. Local recruitment is particularly important in situations where rapidly reaching a sufficient threshold of recruits is critical, such as during initiation of ▶ cooperative transport of food items. It is also used to rapidly mobilize defenses against predators or competitors.

Differential Recruitment and Collective Decision-Making

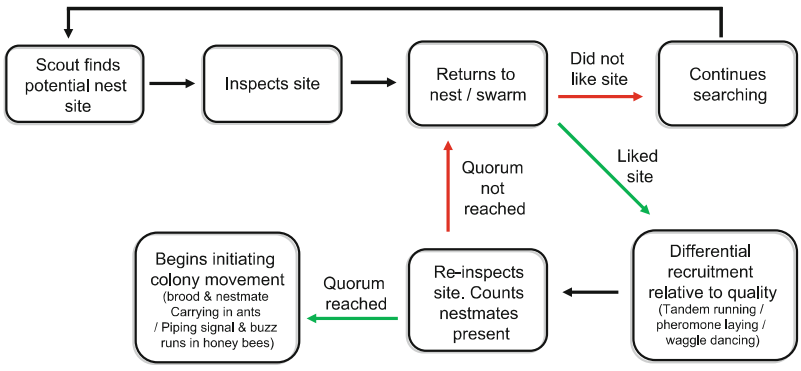
The strength of a recruitment signal is often modulated according to the perceived value of the resource. Better resources result in more waggle dance circuits, more pheromone being deposited on pheromone trails, or a higher probability of initiating tandem running. Recruitment during foraging is usually modulated according to resource quality or quantity and can also be affected by path characteristics, danger level, and individual- and colony-level state.

Differential recruitment can result in colonies making adaptive collective decisions about how many workers to deploy to a resource and which resources to collectively exploit. The mechanism for such collective decision-making is based on positive feedback: a scout locates a resource and recruits to it. As more workers arrive, they in turn recruit, beginning a positive feedback cycle which ends once the food source is fully exploited, whereupon workers that cannot forage stop recruiting, or when a quorum has been reached at a potential nest site (Figs. 3a and 4). The addition of differential recruitment to this positive feedback system results in collective choice. That is, given two simultaneously discovered resources, more recruitment to the better resource will result in more workers exploiting it and themselves recruiting to the better resource. Soon, the poorer resource is outcompeted by the better one (Figs. 2 and 3b).

As this collective decision-making process is based on a positive feedback loop (recruitment → more foraging → more recruitment), noise and stochasticity can play a major role in the ultimate collective decision, since positive feedback will amplify small differences, especially given nonlinear recruitment. This eventually results in symmetry breaking, wherein one option is selected from a range of equally good alternatives. However, while such collective decision-making processes have been demonstrated repeatedly in



Communication: Recruitment to Resources, Fig. 3 Collective decision-making during food recruitment. (**a**) Modulation of forager number relative to the capacity of the resource. (**b**) Choice of a good over poor quality food source. (Adapted from Ref. [4])



Communication: Recruitment to Resources, Fig. 4 The nest site selection process. This schematic shows a generalized case. Additional elements may be present, such as the role of prior scouting in ants or negative feedback and cross-inhibition signals in honey bees. (Adapted from Ref. [2])

the lab (Fig. 2), their applicability to food source selection in the wild is unclear. This is because under most natural circumstances, individual food sources cannot support large numbers of ants, and so positive feedback and a unified choice may be prevented.

While the basics of collective decision-making through recruitment are similar between waggle dance-based recruitment and pheromone recruitment, there are also fundamental differences [5].

Information Content of Recruitment Signals

Successful recruitment requires two components: activating workers to follow the signal (often termed the attractant) and the provision of location information for the resource. In many cases, such as mass recruitment trail pheromones, one signal provides both components. However, in other cases activation and direction can be performed by separate signals, such as two separate pheromones or a motor display for activation and a pheromone trail for direction, with only activated foragers following the trail [10]. In many social insects, such as most social wasps, stingless bees, and bumble bees, only the activation component of recruitment is used, which informs nestmates of the presence of a food source but not its location. Such activation signals are often used in conjunction with ▶ trophallaxis or other food sharing and odor cues on the signaler's body, thereby providing information about the nature and quality of the resource (see below).

Modulatory signals can affect the response of workers to recruitment signals. For example, different motor displays in the African ▶ weaver ant *Oecophylla longinoda* can be used in conjunction with trail pheromone to recruit variously to food, new territory, new nest sites, or intruders [10].

The activation aspect of recruitment signals can interact strongly with individual forager memory and other cues. For example, a honey bee performing a waggle dance to a patch of roses may activate the memory of inactive forager bees that have foraged on roses before. These bees, on smelling the rose odor on the dancing bee, may ignore the directional component of the dance and follow their own route memories to where they had found roses previously [8]. In other words, it suffices for the recruiter to alert experience nestmates that a familiar patch of roses is once again in flower.

Recruitment signals have varying amounts of noise in them, and recruits sense the signal with some error. This may be due to constraints on the system. For example, honey bee waggle dances are noisier when the waggle run is made horizontally, due to gravity pulling the bees body downward. In other cases, noise may be adaptive, in that it allows nearby resources to be discovered.

The Broader Role of Trail Pheromones in Colony Organization

Trail pheromones are the most commonly used recruitment mechanism in social insects and often have a much broader role than simply guiding insects to a resource. They can be employed to modulate the use of different parts of a foraging network, using similar positive feedback mechanisms to those described in Fig. 3b to choose the shortest path to a food source. Negative feedback on pheromone deposition, caused by crowding on the trail or even the presence of pheromone itself, can cap trail strengths and potentially help to route traffic around or over congested parts of the trail network. Importantly, pheromone trails can interact with individual route memories to affect worker behavior. For example, for ants with a memory of a food source, a pheromone trail may act not as a directional signal but rather to reassure the worker that she is going in the right direction. This can allow foragers to run faster and straighter, while also acting as a fail-safe mechanism by informing the forager if she accidentally leaves the correct route. Similarly, pheromone trails may act to support memory-based navigation on complex routes, and pheromone deposition increases after foragers make and correct a navigational error [4].

Pheromone trails are also deployed outside resource-recruitment situations. They may be used as a template around which tunnels and galleries may be constructed. They may be used to partition territories and reduce competition. More exotically, pheromone trails have been argued to be used in order to assess the size of potential nesting cavities by cavity-dwelling ▶ *Temnothorax* ants. The structure of a pheromone trail network can also encode directional information: as outgoing trail bifurcations usually have an angle of c. 50–60°, workers can use them to tell whether they are travelling toward or

away from the nest. Two symmetrical paths at 30° indicate outgoing, while an asymmetrical bifurcation of 30° and 120° indicates returning.

Consensus Decision-Making and House Hunting

When a colony needs to ▶ relocate to a new nest site, it must make a consensus decision about where to move. Recruitment to new nest sites is therefore necessarily more complex than recruitment to food. The initial stages of recruitment to a new nest site are similar to recruitment to a food source. Scouts search the environment for suitable nesting sites and, on finding one, return to the nest and begin recruitment via pheromone trail, tandem running, or waggle dance [2]. Recruitment strength varies according to the perceived quality of the nest site. However, once sufficient individuals have been recruited to a nest site, a quorum is reached, and the nest site choice is finalized. In house-hunting ants, the recruiters begin tandem-carrying workers, as well as brood and finally the queen, to the chosen nest site. In honey bees, recruiters produce piping signals in the swarm, shutting down recruitment waggle dances and preparing the swarm for flight to the chosen nest site [2].

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