



Information flow during social feeding in ant societies

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Summary

In fire ants, social feeding is regulated by two hungers, one among larvae, the other among workers. Workers donate to larvae or to workers hungrier than themselves, and solicit from workers more satiated than themselves. Food flows via a chain of demand initiated by hungry solicitors rather than a chain of transfer initiated by full donors.

Colony patterns of food distribution emerge from the rules by which individuals transfer food. The key elements are the rate and duration of individual food transfers. The rate of transfer is regulated by two groups: (i) a population of diverse workers coarse-tuned by size and to some degree by age, and fine-tuned by crop fullness and food preference to forage, store food, solicit from, or donate to other colony members; and (ii) a population of larvae who regulate their diet by soliciting at rates based upon individual food preference, midgut fullness, and body size. The duration of worker-worker trophallaxis is variable, generating an uneven distribution of crop fullness among workers. Variation in crop fullness contributes to the distribution of worker labor among social feeding tasks. The duration of worker-larva trophallaxis is fixed and brief. The brevity of larval feedings and the rate at which they solicit feedings result in a relatively even distribution of food per unit of larval size. This even distribution contributes to colony growth by diverting excess food to the incoming generation of larvae.

In total, social feeding is a decentralized homeostatic system composed of individuals constantly moving toward fullness. Relatively simple rules of thumb, foraging-for-work algorithms, food-preference templates, cue clouds, negative feedback and self-organizing processes contribute to the interactions between individuals and the distribution of individuals among feeding tasks inside and outside the nest.

Introduction

One of the pressing issues of social insect research is the synthesis of colony organization from the actions of individuals. A number of hypotheses have emerged within the last 2 decades, each attempting to explain information flow among workers, moment to moment, in an ever-changing social environment. Although most describe colony organization as a decentralized process, each hypothesis offers a different mechanism regulating the flow of information. Mechanisms thought to regulate worker behavior and division of labor include polymorphism [1–3, pp. 298–354], learning [4], simple “rule-of-thumb” responses to local cues [5], “foraging-for-work” algorithms [6], random amplification (reviewed in [7, 8]), genetic differences in fixed-response thresholds (reviewed in [9, 10]), temporal/age polyethism (reviewed in [11, p. 400]), social context [12], and stigmergy (Grasse, 1979, cited in [7]). It is possible that, like the parable of the blind men describing different features of the same elephant (poet John G. Saxe, 1816–1887), each mechanism applies to a different feature or a different level of organization in colony life. The intent of this chapter is to review the mechanisms regulating the flow of food among colony members and the flow of colony members among social feeding tasks in an attempt to describe the flow of information therein.

Social feeding

In social feeding, food is the currency that links the majority of colony members and colony tasks to one another. For example, in fire ants, food links the colony to its environment. Food is acquired in quantities that far exceed the metabolic requirements of the individual and is transported from the environment to the nest by a fraction of colony members (W.R. Tschinkel, unpublished data), the foragers. Inside the nest, food links foragers to intermediaries, who store it, share it with still other workers, or feed it to the important end users, the queen and the larvae [13–15]. Food also links brood and soldiers who defend the concentrated supply of newly converted ant tissue from predators. Finally, metabolic waste products may link workers to their nest and to each other. Workers plaster the inside walls of the brood chambers and tunnels with their excretions, providing additional structural support (casual observation). Workers regularly step into the

toilet area where larval excretions are deposited and groom themselves for extended periods of time (casual observation), possibly marking themselves with a common scent used in nestmate recognition. The last decade has seen a great deal of novel research revealing the mechanisms regulating the components of social feeding. A summary of this work follows.

Brood organization

In contrast to bees and wasps that rear larvae individually in small cells, ants rear larvae communally, piled together in relatively large chambers. Brood items are spatially organized in either of two configurations depending upon the species and the complexity of its nest. In founding colonies (*Solenopsis invicta*, casual observation) and in species that nest in a single chamber (*Leptothorax unifasciatus* [16]), brood items are arranged in concentric rings with eggs and microlarvae clustered at the center and surrounded, in progressively larger rings, by larger larvae and pupae. One mechanism regulating this arrangement could be passive, whereby the egg-laying queen occupies a central position with younger brood pushing older brood outward. However, passively generated concentric rings are often destroyed when the queen moves or when the colony migrates within the nest or to a new nest site. If brood organization is adaptive, then workers must be able to restore order after each migration. An active mechanism, with workers sorting brood based on several simple rules [17], could quickly and efficiently reorganize brood. Fire ant workers appear to have a general rule, “cluster all brood items together” followed by a more specific rule, “move like brood item next to like brood item.” Fire ant workers sort brood item by repeatedly antennating first the brood item in its mandibles, then the surrounding brood items until a match (probably odor) is found. At this point, the worker gently places the brood item (egg, larva, prepupa, or pupae) next to the like brood item. The shape, size, and pilosity of fire ant eggs, larvae, and pupae determine their domain of care (defined as the amount of empty space around each brood item [17]). In all probability, these morphological differences in brood items contribute to the concentric arrangement of brood as smaller, more closely packed items naturally become centralized within larger items.

For species building complex nests, brood items are dispersed among many chambers depending upon the microclimate. Eggs and microlarvae are housed

near the queen in humid chambers, older larvae in moderately warm, humid chambers, and pupae in hot, dry chambers [18, 19]. Workers could easily organize brood within and among brood chambers, operating with the original two rules and one or two additional rules for vertical sorting of brood depending upon the microclimate inside the nest. From the worker's point of view, the organization of brood emerges from each worker's response to local cues with a few simple rules of thumb. From the colony's point of view, the allocation of workers to the task of brood sorting is regulated by foraging for work algorithms [6] and negative feedback—fewer workers stop to engage in brood sorting as more brood item matches are completed.

Brood assessment

Once brood items are spatially organized, they are groomed and fed incessantly until the next disturbance or migration. Fire ant workers are tireless caregivers. Each brood item is assessed approximately 700 times per hour or once every 5 s [20]. For larvae, the assessment:feeding ratio is high—on average, larvae are contacted 70 times for every feeding they receive. Similarly, in *Pheidole dentata*, larval feedings occurred, on average, once every 50th behavioral act (2%) by minor workers [21]. Workers achieve constant care of brood by maintaining a high constant density of workers on the brood pile (85% coverage). Worker density remains constant regardless of brood satiation [22], worker:brood ratio or colony size [14]. Although warmer temperature slightly reduces the density of workers on the brood pile, workers move faster, thus maintaining a steady contact rate (D.L. Cassill, unpublished data). Potentially, workers regulate their density by monitoring the time between worker contact [23, 24]. From the colony's point of view, the allocation of workers to the task of brood assessment is regulated by negative feedback at the individual level—workers leave the brood pile when the time between contacts becomes too short.

Another feature of brood care is the great simplification of worker decision making when feeding larvae. During each trophallactic event, a larva is fed a tiny, fixed amount of food (~1.5 nl [25]) regardless of differences in larval size, hunger, orientation, or location on the brood pile. One outcome of a fixed volume is that workers do not have to assess how hungry or how large a larva is and adjust the amount of food they transfer accordingly. Instead, the worker feeding

response is a simple, binary decision—feed or do not feed this larva. The brevity and constancy of worker-larva trophallaxis was found in other ant species as well, suggesting that small food increments are a common feature of larval feeding in ants.

A fourth feature of brood care is that workers frequently switch from one task to another and back again (D.L. Cassill, unpublished data). In theory, if workers were prone to staying on task, a single worker could feed hundreds of larvae each hour, even allowing time for assessment and crop refills [20]. In actuality the average worker feeds fewer than 30 larvae each hour [14]. Such erratic task switching by active workers may be the mechanism that ensures that a large number of workers are foraging-for-work, thus fine-tuning the allocation of workers among multiple tasks. We suggest that “foraging-for-work” algorithms be expanded to include information signals from other colony members as well as inanimate cues from the environment. After all, it is the intense assessment of brood by hundreds of wandering workers that produces the highly reliable brood care system, turning a probability of being fed, groomed, or moved into a certainty. If one worker fails to feed, groom, or move a brood item, another responds shortly thereafter.

Larval hunger

Meal volume is tightly regulated, not by workers, but by the larvae themselves who actively solicit food from workers [22]. Several lines of evidence suggest that the solicitation cue is a nonvolatile chemical—a pheromone or a metabolic waste product—rather than a behavioral or tactile cue. For a fourth-instar larva, a typical meal consists of hundreds of tiny feedings delivered over 8 to 12 h [22, 13]. The rate at which hungry larvae are fed is not affected by larval orientation, its location in the brood pile, or the hunger or size of adjacent larvae. Rather, larvae solicit, and are fed, at rates in proportion to their size and level of hunger. On average, each larva is fed at a similar rate per unit of larval volume such that all larvae are brought to fullness together. Nevertheless, larval appetites vary, resulting in different meal sizes that, in turn, may produce different adult sizes or castes.

We simulated larval hunger [20] to determine which feeding rules affected the patterns of meal size and nutritional mix among larvae. Varying the response

thresholds among workers affects only the total time required to bring larvae to satiation but not the even distribution of food among larvae. When the rate of larval feeding is a function of larval size but not hunger, larvae are brought to fullness evenly over time, but are grossly overfed when food is abundant. When the rate of larval feeding is a function of larval hunger but not size, larvae are not overfed, but some larvae became full far sooner than others. The sum total of the patterns by which larvae solicit for food is that surplus food is retained over the short term inside worker crops. This phenomenon has potential implications for colony growth: surplus food stored in worker crops can act as a buffer against sporadic food availability, keeping a steady flow of food moving to the larvae. This allows more continuous larval feeding and growth, at least on a scale of a few days. Such buffering would also reduce the necessity for cannibalizing larvae to retrieve food during shortages. During periods of food deficit, hunger (the absence of food) is also distributed evenly over the larval population, thus reducing the possibility that some larvae receive no food and starve to death. Reduction of growth would then be spread evenly over all larvae allowing larval numbers to remain constant, offering clear advantages for colony growth when food supplies fluctuate.

Larvae not only regulate food volume but food quality as well [15]. Larvae have independent appetites for food, preferring concentrated rather than diluted solutions, and ingesting food at rates characteristic for that food type or food state, regardless of whether they are empty or full of other food types. Because meals are delivered in tiny morsels by hundreds of workers carrying different nutrients, unmixed, in their crops, each larva can fine-tune the nutritional mix of its diet. This ability provides larvae the potential for regulating their own development in competition with other larvae. Any extrinsic factor that regulates larval appetite (such as temperature or queen inhibitory pheromone; D.L. Cassill, unpublished data) could potentially regulate caste determination.

From the larva's point of view, meal quality is regulated by a food preference template (learned or innate); meal volume is regulated by negative feedback (less food is ingested with satiation). From the worker's point of view, the distribution of food among larvae results from their responding to larval hunger with simple rules of thumb rather than by a central guiding process. From the colony's point of view, the allocation of workers to larval feeding is regulated by negative feedback; as larvae become full, fewer workers are engaged in feeding them. The distribution of food among larvae, a colony-level pattern, emerges from the accu-

mulation of thousands of workers responding independently to the solicitation signal of thousands of larvae at rates determined by their size and hunger. In the final analysis, colony hunger [26] does not exist. At least for larvae, it is an abstraction that generalizes the specific hunger of the individuals within the nest.

Worker motivation

We now focus our attention on the role of the worker in social feeding. Are all workers equally likely to forage, donate to workers, or feed larvae? In ants, young workers almost universally engage in brood and queen care, and move to general nest duties and finally to foraging as they age [8]. Polymorphism also plays a role in the distribution of workers among colony tasks [3, pp. 298–354]. In *Solenopsis invicta*, the tendency to feed larvae declines minimally and unevenly with age [14]. Worker size plays a larger role in motivating individuals to engage in different social feeding tasks. On average, medium-sized workers feed larvae most often, small workers groom larvae most often, and large workers recruit most strongly to food [27, 14].

Worker hunger plays a substantial role in motivating workers to tend brood [14]. Workers initiate feedings to hungry larvae in direct proportion to the volume of food in the workers' crops. Additionally, the type of food that workers ingest affects their feeding decisions. Workers carrying sucrose initially stay off the brood pile and donate crop contents to other workers, whereas workers carrying amino acids move directly to the brood pile to feed larvae [15]. This bifurcation of behavior based on the type of food being carried in their crops suggests a relatively sophisticated level of decision making by workers.

Once workers fill themselves, the timing of their last meal (volume and type) is erased [14], and they respond according to the current contents of their crops. Full workers do not actively push food on other workers. Rather, they advertise, actively by antennating others or passively by remaining stationary with their mandibles open in a stereotypic donor-display posture waiting for soliciting workers to contact them (D.L. Cassill, unpublished data). Howard and Tschinkel [26] claimed that full donors pushed food onto passive recipients. A review of their methods revealed this interpretation to be incorrect. Full foragers ingested less radiolabeled sugar water than did empty foragers. Therefore, less radiolabeled sugar water reached nestmates, not because they fed fewer workers but

because their crop contents were diluted. Altogether, the physiological process initiating the flow of food into the colony appears to be hunger rather than fullness.

Whereas hunger is evenly distributed among larvae, it is unevenly distributed among workers. The uneven distribution of hunger among workers is created by the highly variable frequency and duration of worker-worker trophallaxis [14]. There are significant differences in the quantity of food consumed by nurses, foragers, and reserves [14, 28]. Nurses solicit when empty and donate to larvae or other workers when full. Scouts forage when empty and donate to other workers when full. Reserves solicit or are recruited to food sites when empty and donate or remain inactive when full. Likewise, different food types are unevenly distributed among workers, with small volumes of amino acid solution reaching the most workers and larger volumes of sugar water reaching the fewest workers [29]. The skewed distribution of food volume and food type among workers has been reported for a number of other species (reviewed in [30]), suggesting that it is a fundamental feature of social feeding. The degree of individual worker hunger is an example of a single mechanism generating a distribution of labor from the colony's point of view and an alteration of behavior between foraging, soliciting, or donating from the worker's point of view.

Considerable variation in individual behavior occurs among workers that cannot be attributed to differences in size, age, or hunger [14]. Some nurses feed many larvae; some feed few larvae. Additionally, the same worker may be repelled by contact with larvae one moment (antennae jerk backwards and the worker immediately changes direction) and attracted to them (grooming or feeding) the next (D.L. Cassill, unpublished data). This variation in worker response poses a problem for the fixed response threshold hypothesis [9, 10] (see Beshers and Robinson, this volume, and Bonabeau and Theraulaz, this volume), in which workers are viewed as captive to their neurology, producing a stereotypic response when a cue is sufficiently strong enough to surpass a worker's perception threshold. We propose an alternative, a cue cloud hypothesis in which workers are capable of perceiving cues regardless of their intensity, and actively choose to respond to one particular cue among a suite of perceived cues. The parameters that shape an individual's cue cloud may vary depending upon extrinsic factors such as social context (cue clouds change moment to moment as workers wander about the nest or territory) and on intrinsic factors such as a worker's size, age or hunger. The internal state changes regulating worker moti-

vation are unknown and offer an interesting opportunity for the field of social neurology and endocrinology.

Forager hunger

Foragers do not respond directly to the nutritional needs of larvae. When foragers and reserves are hungry, the presence or absence of larvae does not affect recruitment to food sites [14]. Starved nurses actively solicit food from reserves, which increases food solicitation by reserves and foraging activity by foragers [31]. Likewise, in the ant *Myrmica rubra*, hungry nurses cause foragers to ingest more food than they will if nurses are full—the influence is not reciprocal [32]. From the above, it is apparent that the mechanism by which larvae communicate their need for protein to foragers is indirect. Larvae act as a protein sink [33] and are fed protein by nurses, creating a protein hunger that reverberates from nurses to reserves to foragers who forage for protein outside the nest. Likewise, workers inside the nest act as a sugar sink, creating a hunger for sugar in the foragers which motivates them to leave the nest to forage for more sugar.

Foragers influence larval nutrition by selecting which food they transport back to the nest. Upon encountering food outside the nest, workers evaluate its quality, then return to the nest and recruit other workers by antennating a variable number of workers depending upon their enthusiasm for the food find (*Pheidole* [34]; *S. invicta*, D. L. Cassill, casual observation). When starved as a group, foragers and reserves consistently recruit to different food types at characteristic rates, recruiting twice as strongly to sucrose as to amino acids solutions. When a colony becomes satiated on one food type, such as sugar water, fewer workers will recruit to it again but will recruit strongly to amino acid solution and *vice versa* [14]. This ability to discriminate food types may be the cause of the idiosyncratic colony food preferences in fire ants observed by Glunn et al. [35]. The mechanism for food preference is thought to lie in the individual's ability to discriminate based upon some learned or innate understanding of food value rather than by comparison shopping among available food (*Pheidole* [34, 36] *Apis mellifera* [24, 37, 38]). Foragers may reject several food finds (casual observation) before ingesting and will ingest from only one food site before returning to the nest [15]. Additionally, foragers pass food on to a clique of workers in a chain reaction that usually involves one bout of solicitation before that worker becomes

a donor. The advantage of small discrete feedings by workers carrying unmixed nutrients in their crops is that individual larvae can fine-tune the nutritional mix of their meal.

The self-organization (positive reinforcement from random amplification) of foraging trails has been well described for species that mass-recruit to food sites [39–41]. In *Pheidole pallidula*, differential response thresholds between castes are thought to affect which ants follow recruitment trails [42]. In fire ants, returning scouts advertise the food quality or novelty with high tempo movement and donor displays (D.L. Cassill and L.E. Chase, unpublished data). These behaviors regulate the number of recruits that leave the nest. Trail pheromone then guides recruits to the food source. Once at the food source, workers decide individually to reject and begin a random search elsewhere or to ingest and return to the nest. Initially, group movement along a trail is a positively reinforced process that can result in leading workers to a low-quality food source [43]. Ultimately, however, group movement along trails is regulated by negative feedback; as food resources run out, trail formation diminishes to that site (reviewed in [44]).

Conclusion

In the final analysis, social feeding is a decentralized, homeostatic process organized by hunger and bound by food exchange. Interactions are initiated by hungry individuals soliciting food from full donors in a chain of demand. The transactions of this chain of demand, based on individual hunger, an ability to discriminate food quality and novelty, plastic motivation levels, simple rules of thumb and foraging-for-work algorithms, are the foundation of the distribution of workers among social feeding tasks. No single worker possesses an overview of the nutritional status of either larvae or other workers. Rather, colony nutrition is an emergent property, the product of thousands of individuals (workers and larvae) independently adjusting their rates of ingestion based upon the food choices they encounter and their current appetites for that food.

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