Individual Complexity and Self-Organization in Foraging by Leaf-Cutting Ants

FLAVIO ROCES

Zoologie II, Universität Würzburg, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

Abstract. Leaf-cutting ants cut vegetation into small fragments that they transport to the nest, where a symbiotic fungus cultivated by the ants processes the material. Since the harvested leaf fragments are incorporated into the fungus garden and not directly consumed by the workers, it is expected that foraging workers select plants by responding to those physical or chemical traits that promote maximal fungal growth, irrespective of the potential direct effects of these leaf features on them. In this paper I summarize experimental work focusing on the decision-making processes that occur at the individual level, and discuss to what extent individual complexity contributes to the emergence of collective foraging patterns. Although some basic features of self-organizing systems, such as the existence of regulatory positive and negative feedback loops, are expected to be involved in the collective organization of leaf-cutting ant foraging, I contend that they are combined with complex individual responses that may result from the integration of local information during food collection with an assessment of colony conditions.

Social Foraging in Leaf-Cutting Ants: Self-Organized?

Leaf-cutting ants are the dominant herbivores in the Neotropics. They cut vegetation into small fragments that they transport to the nest, which may contain over a million workers. To support these large colonies, workers search out and harvest plant species that are suitable for the development of the colony’s resident symbiotic fungus. Adults obtain more than 90% of their energy requirements during foraging from the plant sap of the cut material (Littledyke and Cherrett, 1976). The fungus garden, which represents the sole food source of the developing brood, appears to be responsible for the ability of the ants to utilize most of the available plant species. Since the harvested leaf fragments are incorporated into the fungus garden and not directly consumed by the workers, it is conceivable that ants and fungus have conflicting requirements for the quality of the plants to be harvested. On the one hand, ant workers may prefer resources that support maximal rates of fungus growth, more or less irrespective of the attractiveness of the plant sap being imbibed during the harvesting process. On the other hand, workers may base decisions about the quality of a given resource on the immediate availability of energy to support their foraging activity. Given these two different demands, the herbivory patterns of leaf-cutting ants can be understood only by investigating the measures used by foraging workers when making decisions and the extent to which the behavior of the individuals is influenced by the state of the symbiotic fungus. For that, emphasis should be put on both the kind of information workers use during foraging and the integration of individual responses that results in the emergence of a collective pattern. Leaf-cutting ants appear to be well suited to analyze this interplay between individual and social aspects of foraging. At the individual level, information is available about the rules used by workers to decide on the size of the leaf fragment to be cut (Roces, 1990a; Wetterer, 1990, 1991a; Burd, 1995, 1996). At the colony level, studies have provided details about plant selection and foraging activity of colonies in the field (e.g., Howard, 1990, 1991; Nichols-Orians and Schultz, 1990).

In trying to understand the contribution of regulated, self-organizing processes to the emergence of collective foraging patterns in colonies of leaf-cutting ants, it is im-

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E-mail: roces@biozentrum.uni-wuerzburg.de

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portant first to draw attention to three features of the colony-level foraging patterns that would not, \textit{a priori}, be expected. First, workers show strong preferences for a few plant species but persist in harvesting numerous species that remain, in a consistent way, only slightly preferred (Rockwood, 1976). Second, plants are usually abandoned before they are completely defoliated, even those that are ranked among the most preferred (Cherrett, 1968; Fowler and Stiles, 1980). Third, ants travel long distances on foraging trails to reach plant resources, with individual round-trips lasting several hours; and they bypass conspecific plants of apparently equal quality located much closer to the colony (Cherrett, 1983).

To explain such complex foraging patterns, three hypotheses have been advanced. The optimal foraging hypothesis (Fowler and Stiles, 1980; Rockwood and Hubbell, 1987) suggests that the observed patterns are the result of workers foraging to maximize the rate of resource delivery. According to that reasoning, a distant plant of moderate quality located close to an existing foraging trail may provide a higher return than a nearby plant of much higher quality, but at some distance from a trail. Thus workers may abandon plants being harvested when a new plant offering a higher rate of return is found. The resource conservation hypothesis (Cherrett, 1983) suggests that the ants limit the damage caused to highly preferred or nearby resources, thus conservatively managing resources over the lifespan of their colony. Finally, the nutrient balance hypothesis (Powell and Stradling, 1991; Stradling and Powell, 1992) contends that the harvested resources represent a complementary diet for the symbiotic fungus, so that ants are expected to seek out a variety of plants to provide the fungus with an appropriate mix of nutrients and to avoid high levels of any single toxic secondary plant compound.

As predicted by Howard (1991), it has proven difficult to evaluate the extent to which colony-level foraging patterns are uniquely explained by any one of these hypotheses. Moreover, the mechanisms underlying the short- and long-term dynamics of plant selectivity are completely unknown. Are self-organizing processes able to account for such complexity in pattern formation, without the need to invoke complexity in the decision-making processes at the individual level? In recent years, investigations of self-organization in biological systems have suggested that social insect colonies often work as a decentralized system composed of cooperative, more or less autonomous units distributed in the environment that manage local information and exhibit simple probabilistic stimulus-response behavior (Bonabeau \textit{et al.}, 1997). My present contribution focuses on both the decision-making processes observed in individual leaf-cutting ant workers and the integration of individual behavior into colony function. I shall first describe the kind of information single workers use to make decisions about resource quality, and then discuss the emergence of collective patterns and to what extent regulatory, self-organizing processes may be involved.

**Decision Making During Foraging: Individual Complexity**

In the field, scout workers from a colony of leaf-cutting ants search for suitable resources and, upon discovery, they decide whether a given resource is worth communicating to other nestmates. Plant selectivity is mainly based on both chemical and physical features of the leaves (Howard, 1987; Nichols-Orians and Schultz, 1990). If the source is attractive, workers may decide to return to the nest, laying a chemical trail, or to cut a fragment and carry it back to the nest. Polymorphic leaf-cutting ant foragers frequently harvest leaf pieces that correspond in mass to that of their own bodies (Lutz, 1929; Cherrett, 1972). This, in part, results from the geometric method of leaf cutting. Since workers anchor on the leaf edge by their hind legs and pivot around them while cutting arcs out of the leaves, the load-size selected may be directly determined by a fixed reach while cutting, dependent on worker body size (Weber, 1972). However, there is evidence that not all workers cut fragments as large as they are able to, which suggests a more flexible mechanism of load-size selection in leaf-cutting ants. For instance, foraging distance was shown to affect load-size selection in \textit{Acromyrmex lundi}—ants cut larger fragments farther from the nest (Roces, 1990a)—but not in \textit{Atta cephalotes} (Wetterer, 1991b). For an ant of a given size, Cherrett (1972), Rudolph and Loudon (1986), Roces and Hölldobler (1994), and Burd (1995) found a negative correlation between leaf area density (leaf mass/leaf area) and the size of the harvested fragment.

To understand these decision rules, it should be emphasized that in species with recruitment communication, foraging behavior includes not only the collection of food but also the transmission of information about its location and quality. Because colony food intake is increased through recruitment communication, even at the expense of reduced foraging performance of the individuals, there may be a trade-off between time spent either in acquiring food or in recruiting nestmates, especially during the initial phase of exploiting a food source. This interplay between food-collection behavior and recruitment behavior was analyzed in leaf-cutting ants under controlled experimental conditions (Roces, 1993; Roces and Núñez, 1993). The question of whether the information about food quality obtained during recruitment communication influences the cutting behavior of recruited workers was addressed in an attempt to integrate individual behavior into colony function. Attention was not centered on the successful scout ant that initiated recruitment, but on the behavior of recruited workers that were confronted with standardized stimuli rather than with the original food source. Their responses to these stimuli
were compared after they were informed about food sources of different qualities.

The rationale of the experimental approach was as follows: in independent assays, scout workers of the leaf-cutting ant *Acromyrmex lundi* were first exposed to droplets of scented sugar solution of either 1% or 10% sucrose. Scouts detected these droplets and returned to the colony, leaving a chemical recruiting trail. When the recruited workers arrived, they encountered, not sugar solution, but sheets of Parafilm impregnated with the same scent, containing no sugar. Since all recruited workers found the same standardized material (Parafilm as a pseudo-leaf), differences in cutting behavior between the groups must be the result of the information transmitted by the scout worker that initially found the sugar solution (Roces and Núñez, 1993).

Several behavioral parameters of the recruited workers were observed to depend on the information about food quality they received from a single recruiting scout. Workers recruited by scouts that found 10% sucrose will be referred to as “10%-workers,” and those recruited by scouts that found 1% sucrose as “1%-workers”, but it should remain clear that both groups encountered a sugar-free pseudo-leaf at the source. The 10%-workers (i.e., those recruited to the better food source) cut smaller fragments of Parafilm, returned to the nest at higher velocities, and displayed more active recruiting behavior (by laying chemical trails) than 1%-workers. In another experiment, recruited workers were confronted with small pieces of paper of a homogeneous size. They still traveled at a faster pace if they had been recruited by 10%-scouts, indicating that the differences in speed found in the previous experiment were not caused by differences in loading. More interesting, greater velocity did not compensate for the reduction in fragment size: 10%-workers, despite their higher velocity, showed a lower rate of leaf transport to the nest than 1%-workers (Roces and Núñez, 1993).

These results contradicted the most obvious functional hypotheses and led to a vivid discussion (Kacelnik, 1993; Clark, 1994; Roces, 1994a; Ydenberg and Schmid-Hempel, 1994). Different hypotheses were examined. The “delivery rate maximization hypothesis” would suggest that a behavioral strategy leading to maximum rate of leaf delivery is independent of real or expected sugar content. Since 10%- and 1%-workers behaved in a different manner when cutting the pseudo-leaf, they could not have maximized leaf delivery rate in both treatments. Workers could, however, have been maximizing a compromise between leaf delivery rate and some unknown costs associated with travel speed. If such a cost exists, 10%-workers may pay it (i.e., may run faster) if the value of the food source is greater. Thus they would achieve a higher rate of leaf delivery for a high-quality resource. Indeed, 10%-workers were observed to run faster, but why did they cut smaller fragments? The outlined hypothesis failed to explain these changes in cutting behavior.

An alternative hypothesis, called the “information transfer hypothesis,” (Roces and Núñez, 1993) focused on the recruitment strategies of workers, and was based on the original proposition advanced by Núñez (1982) when analyzing partial crop-filling and foraging behavior in honey bees (see also Varjú and Núñez, 1991, 1993; Schmid-Hempel, 1993, for a detailed discussion about honey bee foraging). The idea was that the decision to transfer information about a newly discovered food source motivates a worker to shorten its cutting behavior and to return to the nest sooner to recruit additional nestmates. A worker sacrifices its individual leaf delivery rate, but the colony as a whole increases its harvesting rate due to the recruited workers that joined in the resource-gathering activity (Roces and Núñez, 1993). This hypothesis was consistent with the higher travel speed and the reduced leaf fragment size in 10%-workers. By cutting smaller fragments, 10%-workers saved cutting time; and by increasing speed, they saved travel time. This hypothesis could, in addition, accommodate the more intense trail-marking behavior observed in 10%-workers.

Further support for the information transfer hypothesis was obtained by analyzing the behavior of recruited workers in more detail, addressing the changes in worker responses after the perception of recruitment signals (Roces, 1993). The behavioral responses of recruited workers have rarely been investigated in ants (Beckers et al., 1992), despite the fact that they are responsible for the amplification and establishment of a recruitment process. The experimental approach was similar to that outlined above. Attention was not centered on the successful scout ant that initiated recruitment, but on the behavior of recruited workers that were confronted with standardized stimuli rather than with the original food source. Their responses to these stimuli were compared after they were informed about food sources of different qualities. Scout workers of the leaf-cutting ant *Acromyrmex lundi* were first exposed to droplets of scented sucrose solution of different concentrations. Once at the source, recruited workers encountered, not sugar solution, but standardized paper discs impregnated with the same scent. Paper discs were either untreated or had sugar added in order to increase their quality. Comparison between assays using untreated and sugared discs of the same weight allowed a distinction between workers’ responses based on the information they obtained during recruitment (which was similar for workers recruited to a given sucrose solution), and those that resulted from their actual evaluation of the disc quality (untreated or sugared disc). In a subsequent experimental series, paper discs of different masses were offered to analyze the effects of load mass on foraging decisions (Roces, 1993).

The information about resource quality transferred by a
single scout ant had several effects on the behavioral responses of recruited workers. The more concentrated the solution found by the initial scout, the faster the recruited workers ran to the source, even though they had no contact with the sucrose solution. After collecting the standardized (untreated) paper discs, the workers also ran faster, the more concentrated the sugar solution initially found by the scout ant. In other words, travel speed of recruited workers to and from the nest depended on the information they received about resource quality. As intuitively expected, disc-laden workers ran more slowly than outbound workers. This reduction in speed, however, could not be attributed to the effects of the load itself, since workers collecting discs of the same weight, but with sugar added, ran as rapidly as outbound, unladen workers.

Workers collecting sugared discs were observed to reinforce the chemical trail on their way to the nest. The percentage of trail-layers was higher when workers were recruited to 10% sugar solution than to 1%, despite the collection of the same kind of discs at the source. These facts indicate that workers’ own evaluation of resource quality depended on the perception of recruitment signals. Such differences in responsiveness to the same stimulus (a given sugared disc) can therefore be attributed to variations in the worker’s motivational state as a result of the information they received during recruitment (Roces, 1993).

The observed decrease in speed after the collection of a nonsugared disc, which could be intuitively attributed to an effect of the load carried, turned out to be the result of a reduced motivation of workers to carry such a material when they have been informed about a high-quality resource (a given sugar solution). That the load itself had no effect on velocity was demonstrated when workers recruited to the same sugar solutions collected sugared discs of the same weight. In this situation, no reduction in velocity was observed. The reduction in speed suggests, therefore, that workers, through the information received during recruitment, may have expected to find a resource of a given quality, and their expectation was not confirmed by the collection of a nonsugared disc. Even when workers were recruited to a sugar concentration of 50%, to which they ran with the highest speed recorded, they never reinforced the chemical trail after the collection of a standard, nonsugared disc, and their velocity turned out to be lower after collection. Those that found sweet discs of the same weight, however, reinforced the trail, and showed no reduction in speed (Roces, 1993).

These results point out the importance of considering the motivational state of foraging workers when their behavior is under scrutiny. This aspect has been largely disregarded in the literature on insect behavior, despite early observations that flight velocity of outgoing (unladen) honey bees depends on the concentration of the sugar solution they collect (Frisch and Lindauer, 1955). Changes in the workers’ motivational state that depend on differences in resource quality are also suggested from measurements in honey bees collecting at different flow rates of sugar solution (Núñez, 1982; Balderrama et al., 1992; Moffait, 2000) or sugar solutions of different concentrations (Seeley, 1986; Stabentheiner and Hagmüller, 1991).

Why do recruited workers run faster when they have been informed about a richer source? The adaptive value of this response might be assigned to the importance of a rapid transmission of information about a newly discovered food source. Workers arriving earlier to the nest can induce nestmates to follow the trail, for instance via tactile stimulation. At the initial phases of trail development, saving time would be of great importance, in order to monopolize a food source as soon as possible. The evaluation of resource quality by recruited workers and, therefore, the probability of reinforcing the chemical trail are, in part, dependent on the information they received: that is, recruits seem to partially rely on the decisions of the first successful ants to amplify a recruitment process. That their decisions appear to be “channeled” by those of the scouts, which may be responsible for the integration of local signals with more general information about resource quality and colony (fungus) conditions, remains to be investigated (see below). This interindividual variability during decision making (see also Jaffé et al., 1985) may be related to both the complexity of food assessment by leaf-cutting ants and the need for rapid responses to monopolize newly discovered sources.

As mentioned above, Acromyrmex lundii workers recruited to rich food sources cut smaller fragments than those recruited to poorer ones (Roces and Núñez, 1993), although both groups found the same standard material at the source. This behavior, unexpected from an individual point of view, also indicates that, in the initial phases of trail development, workers rely in part on the decisions made by the first successful scout workers. By cutting smaller fragments, they save time at the source and run back sooner to inform about it through reinforcement of the chemical trail (Roces and Núñez, 1993); this decision-making system ensures a rapid build-up of workers to exploit the discovered source. That this complexity in individual decision making indeed affects the development of colony-level foraging patterns was demonstrated under controlled laboratory conditions by comparing the foraging behavior of satiated and harvesting-deprived workers (Roces and Hölldobler, 1994). Harvesting-deprived workers cut smaller leaf fragments than did satiated workers, a fact that appears counter-intuitive at the individual level. This reduction in fragment size was observed only in the initial phases of a recruitment process, when information about the discovery is worth transferring. And in fact, these responses correlated with the intensity of recruitment: harvesting-deprived workers showed higher recruitment rates than did satiated workers (Roces and Hölldobler, 1994).
Individual Behavior and Colony Function

As discussed above, leaf-cutting ant workers are central-place foragers (Orlans and Pearson, 1979), since they deliver resources to the nest. As a consequence, they may be expected to maximize the rate of resource delivery to this central place. For social insects in general, the analysis of worker responses in the framework of optimality theory is particularly complex because the maximizing agent is the colony as a whole and not necessarily each individual worker. Thus, if the foraging performance of the colony is enhanced through recruitment communication, one could expect a trade-off between time spent by the individuals in collecting food and time spent recruiting, even at the expense of a reduction in the foraging performance of the individual. In fact, it has been shown that leaf-cutting ant workers rarely maximize either their individual gross rate of leaf delivery to the nest or their individual energetic efficiency (Roces and Núñez, 1993; Burd, 1996), suggesting that performance is maximized at the colony level.

Interpretation of individual foraging performance, and particularly its extension to assess foraging efficiency at the colony level, is further complicated by the fact that a considerable percentage of leaf-cutting ant workers on an active foraging trail return to the nest unladen (between 13% and 75%; Hodgson, 1955; Cherrett, 1972; Lugo et al., 1973; Lewis et al., 1974b). Although a number of these unladen workers can be involved in trail-clearing (Daguerre, 1945) or transport of plant sap (Stradling, 1978), others seem to be engaged in the reinforcement of the chemical trail or in a combination of recruiting and food transport (Jaffé and Howse, 1979). In addition, worker responses may differ at different times during the beginning of a daily foraging cycle (laboratory experiments: Roces and Hölldobler, 1994; field experiments: Bollazzi and Roces, 2001), or when foraging behavior is scrutinized along established foraging trails (Burd, 2000) where the role of recruitment communication in regulating collective foraging has not been clearly understood.

How are the individual responses integrated to generate a collective response? At the colony level, foraging patterns and the selection of suitable plants are particularly complex. Mature colonies have a number of well-established foraging trails that radiate from the nest. Several trails leading to different plants are usually active during a daily foraging cycle (Cherrett, 1968), with outgoing workers leaving the nest using these different trails more or less simultaneously (Lutz, 1929). It is unclear what kind of environmental cues, colony cues, or both trigger the start of a daily foraging cycle (Lewis et al., 1974a,b). Simultaneous exploitation of different food sources has been observed in large colonies of several social insects. For honey bees and ants, it has been shown that self-organizing processes are involved in the collective choice between two simultaneously available patches that differ in quality (Beckers et al., 1990; Seeley et al., 1991). Such collective decision making works well, even though individual workers manage local information and do not directly compare the two alternatives. Laboratory colonies of leaf-cutting ants, over very short distances of at most 1 meter, rapidly exploit available resources and select the most attractive one (Jaffé and Howse, 1979), with the collective patterns being reproduced by models based on simple decision rules and regulatory feedback mechanisms (Jaffé, 1980). Such “explosive” processes may be relevant under these reduced conditions, but may play a minor role under field conditions. In the field, colonies of leaf-cutting ants were observed to repeatedly attack the same individual plants over days, without completely defoliating them, and then move on to others, returning to the former ones after several days (Shepherd, 1982). Taken together, trail fidelity by workers and the long time intervals that mediate the changes in foraging activity along particular trails (in the range of days or weeks) make it unlikely that plant selectivity is based on competing self-organizing foraging processes that occur at the nest, as has been described for a small number of ant species under controlled laboratory conditions (e.g., Beckers et al., 1990). It is more likely that scout workers visiting different food sources at the end of, or close to, existing trails may base their decision on whether to lay chemical trails on both the resource quality actually perceived and on the information about colony needs.

It is still unclear how foraging workers assess (and respond to) the state of the symbiotic fungus. Recent evidence indicates that changes in plant selectivity by workers strongly depend on the effects of the previously collected material on fungal growth, suggesting that foraging workers manage information about the actual state of their symbiotic fungus when selecting a plant outside the nest (see below). Since foraging workers do not directly process the collected leaf fragments, but instead transfer them to a “working chain” inside the nest, their responses are expected to be ultimately controlled by regulatory feedback loops involving information transfer between fungus and gardening workers, and between gardening workers and foragers.
Perspective

Plant material harmful to the fungus may cause foraging workers to cease harvesting of these plants. Once the colony has commenced rejecting a particular plant material, it will continue to refuse it for days or even weeks, a phenomenon called “delayed rejection” (Knapp et al., 1990). As mentioned above, it has been demonstrated that leaf-cutting ants learn to reject plant material that contains chemicals harmful to the fungus (Ridley et al., 1996; North et al., 1997). Ridley et al. (1996) provided bait containing a fungicide, which was initially carried into the nest by the foragers. Eventually, workers stopped foraging on the bait, and this rejection was maintained for weeks. Interestingly, these colonies also rejected bait that contained no fungicide, so that the authors hypothesized that if the substrate causes toxic effects on the fungus, the fungus will produce a chemical signal that acts as a negative reinforcement to the ant servicing that particular fungus garden. North et al., (1999) attempted to trace the pathway of this putative fungal signal. Their results suggest that a signal produced by the fungus does not affect the foragers directly, but indirectly via nest workers that interact with the fungus. Indeed, some of their results suggest that the information is transferred from smaller fungus-garden workers to the larger foraging workers. This putative chemical signal produced by the fungus has not been identified, and the authors discuss an alternative hypothesis that rejection may occur when ants detect fungal breakdown products from unhealthy or dead fungus. The workers would then associate dead fungus with the flavors of the treated bait. In fact, it is known that leaf-cutting ants learn the odors associated with food (Roces, 1990b, 1994b; Howard et al., 1996).

These considerations show that we are far from understanding the regulation of foraging behavior and the emergence of collective, colony-level responses. Although some basic features of self-organizing systems, such as the existence of regulatory positive and negative feedback loops, are expected to be involved in the collective organization of foraging by leaf-cutting ants (Jaffé and Howse, 1979), individual responses appear to be particularly complex. And this seems also to be the case for the organization of social foraging in fire ants, which was described 40 years ago (Wilson, 1962) and has repeatedly been discussed as an example of decentralized colonial decision making. Even though collective responses (“mass recruitment”) are organized by information transmitted from one group of individuals to another, recent evidence indicates that individual ants are able to display a complex array of modulatory communication signals that influence the development of such collective responses (Cassill, 2001).

As recently asserted by Deneubourg et al. (1999), self-organization and individual complexity need not be mutually exclusive processes. I propose that, to understand to what extent individual complexity contributes to generating a collective pattern, we should rise to the challenge of integrating theoretical arguments with empirical research, focusing on the precise mechanisms underlying individual decision making and collective responses in large ant colonies. In particular, elucidating how leaf-cutting ants perceive changes in fungal productivity and use this information to alter their own quality criteria for plant selection remains a major challenge in understanding their individual foraging behavior, and ultimately their herbivory patterns.

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