

Complexity of Environment and Parsimony of Decision Rules in Insect Societies

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Abstract. This paper shows how colonies of social insects process information and solve problems in a complex environment, while keeping some parsimony at the level of the individuals' decision rules. Two studies on ant foraging reveal the diversity of adaptive colony-level patterns that can be generated through self-organization, based on the same individual-level recruitment rules. Regarding prey scavenging, the “ability to retrieve the prey” rule accounts for changes in foraging patterns, with increasing prey size, that show all stages intermediate between an individual and a mass exploitation of food resources. Regarding liquid food foraging, the “ability to ingest a desired volume” rule enables a colony to adjust the number of tending ants to the honeydew production of aphids. In both cases, decision rules are based on intelligent criteria that intrinsically integrate information on multiple variables that are relevant to the ants. Furthermore, the environment can contribute directly to the emergence of collective patterns, independently of any individual behavioral changes. Each environmental factor, including abiotic ones, that alters the dynamics of information transfer in group-living animals should be reconsidered not simply as a constraint but also as a part of the decision-making process and as an agent that shapes the collective pattern.

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Introduction

The Darwinian fitness of animals depends on their ability to assess their environment and to decide accordingly which behavior is the most appropriate. Ideally, group foragers—including social insects—should measure all relevant parameters and process information related to environmental resources and colony needs in order to optimize their foraging decisions. (For an optimization approach to foraging in vertebrates see, for example, Krebs and Davies, 1991; Giraldeau and Caraco, 2000; in social insects, see Oster and Wilson, 1978; Schmid-Hempel *et al.*, 1985.) However, in an ever-changing environment, there may be an advantage to making rapid decisions instead of perfectly informed ones based on multiple time-consuming assessments. Furthermore, one can hypothesize that mechanisms have been selected that enable animal societies to adaptively respond to a complex environment, despite some simplicity of decision rules at the individual level. Self-organization is a means to generate such diversity, flexibility, and complexity of collective responses from interacting individuals that follow simple behavioral rules based on local information (Camazine *et al.*, 2001).

The present essay illustrates how self-organized insect societies adjust their collective response and track the complexity and the diversity of the environment while showing some parsimony of decision rules at the individual level. The following related questions will be addressed in the context of ants' foraging. How many different patterns can be produced with the same behavioral rules? How do ant societies cope with the complexity of their environment? Is decision making based on assessments of multiple parameters or of only a few relevant criteria? Can the environment generate some of the diversity in collective foraging patterns, without behavioral change by the individuals?

Diversity of Foraging Patterns and Parsimony of Recruitment Decision Rules

Ant societies exhibit a high diversity of foraging patterns that allow them to exploit resources efficiently, meet internal needs, and face environmental constraints. Ant scouts are widely recognized as the primary agents that determine the foraging choices of the whole colony since they decide whether or not to lay a trail, and they modulate the intensity of their recruiting behavior according to food characteristics (for a review see Hölldobler and Wilson, 1990; Traniello and Robson, 1995; Detrain *et al.*, 1999). Though essential for understanding the link between individual and collective behaviors, decision-making processes related to information transfer have scarcely been investigated through specifically designed research protocols (see Roces, 2002). Two studies on foraging, for prey or liquid food sources, illustrate how the same decision rule, when operating under different conditions, can give rise to different foraging patterns in ant societies.

The first study (Detrain and Deneubourg, 1997) was carried out on the dimorphic ant *Pheidole pallidula*, characterized by two morphologically distinct castes of workers (minor and major). Members of this species scavenge on various sizes of insect prey and exhibit different foraging patterns ranging from an individual retrieval of small prey to a mass exploitation of large prey by a well-defined foraging trail. We demonstrated that the resistance of prey to traction, and its associated retrievability, governs the decision of the forager to recruit nestmates. Indeed, by simply preventing ants from moving a small prey away (e.g., fruit flies pinned down on the substrate or placed under a net), one can artificially increase the recruitment trail intensity to a value similar to that observed for a large prey item (e.g., a cockroach). This simple decision rule based on prey retrievability generates all the major scavenging patterns of the ant species, as shown by the following algorithm (Fig. 1). Success in prey carrying stimulates the forager to move on and lay only a weak trail on its way back to the nest; this results in the individual exploitation of small prey. When these small food items are numerous and aggregated, weak but frequent reinforcements of the trail lead to a slow and progressive monopolization of the source. Failure to retrieve the prey item is followed by an intense trail-laying that mobilizes additional foragers to the discovery site. Recruited ants can then either retrieve the prey collectively or, if still unsuccessful, dissect it on the spot and suck the hemolymph. Majors, which show a higher response threshold to recruitment stimuli, are mobilized only to large prey items when the trail is strongly reinforced and highly concentrated. The powerful mandibles of those large-headed foragers then facilitate the cutting of the prey. In sum, the same decision rule generates several foraging strategies that differ in their level of cooperation between

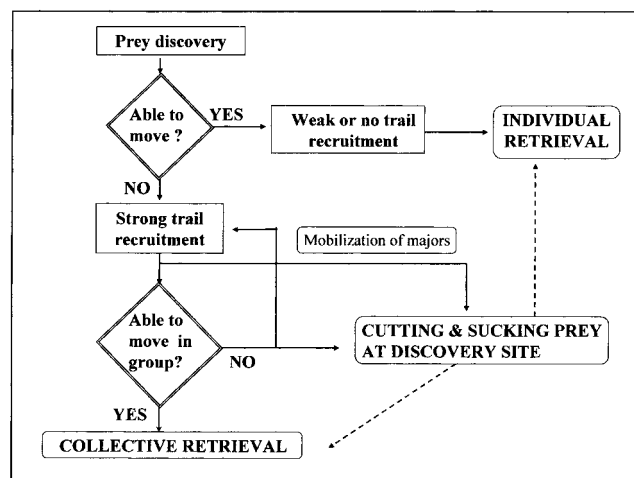


Figure 1. Algorithm and decision-making process followed by the ants during prey scavenging. Redrawn from Detrain and Deneubourg, 1997.

workers and leads to the emergence of the scavenging strategy best suited to the circumstances.

In the second study (Mailleux *et al.*, 2000), the foraging strategies of ants exploiting sugary liquid sources such as aphid honeydew were investigated by comparing the behavior of *Lasius niger* scouts at sucrose droplets of different volumes. When the food volume delivered exceeds the capacity of a worker ant's crop, nearly all scouts (90%) lay a recruitment trail. When a smaller droplet is offered, several scouts return to the nest without laying a trail. The percentage of trail-layers decreases with the droplet size, but the number of chemical marks emitted by each trail-laying ant does not change. The key criterion the scout uses to start laying a recruitment trail is her ability to ingest a desired volume, independently of the time spent drinking. This volume is not a fixed value shared by all scouts but varies from one ant to another. Desired volumes act as thresholds that are normally distributed (see also Page *et al.*, 1998; Beshers and Fewell, 2001). The "ability to ingest a desired volume" rule accounts for the collective regulation of foraging to the amount of food available, as shown by the following algorithm (Fig. 2). If the ant is able to ingest its desired volume, it lays a trail and recruits nestmates. If it cannot obtain its desired volume due to small droplet size, food depletion, or crowding at the food site, it searches for additional droplets in the foraging area. If unsuccessful, it goes back to the nest without laying a trail. This "desired volume" decision rule allows the colony to adjust the number of tending ants to the honeydew production of aphid colonies. Hence, information about the droplet size is not represented at the individual level but rather at a group level, through the fraction of trail-layers among returning ants.

These two studies of ant foraging reveal that, in the absence of centralized control, collective problem-solving

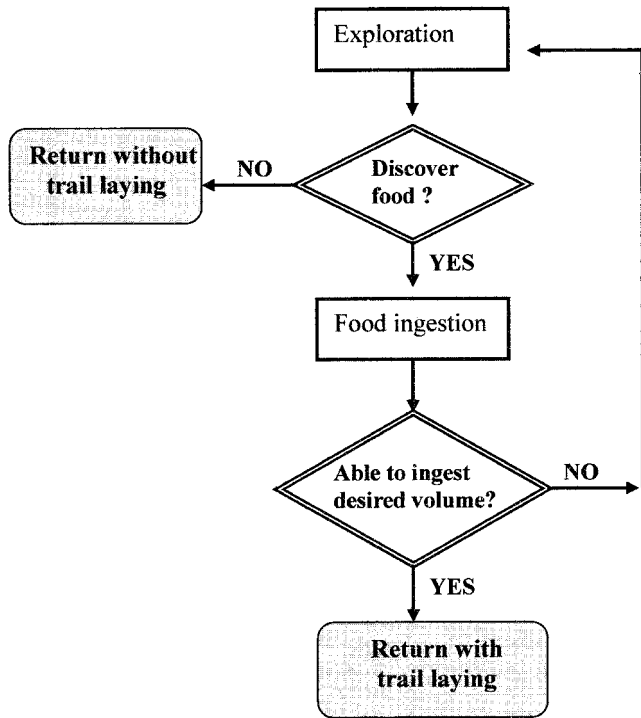


Figure 2. Algorithm and decision-making processes followed by the ants when exploiting liquid food sources. Drawn from results of Maillieux *et al.*, 2000.

and foraging strategies can emerge through simple rules for information transfer between individuals. Moreover, in multiple-source situations, the same behavioral rule can produce different group-level patterns of exploitation: these range from a scattering of foragers over all food items to a focus on one or a few food sources (Nicolis and Deneubourg, 1999).

The Concept of Intelligent Decision Criteria

One way for insect societies to cope with the complexity of their environment is the use of intelligent decision criteria at the individual level. Intelligent decision criteria do not require the ant to make some complex and precise assessment of all environmental parameters; instead, they rely on cues that automatically integrate several variables (inside or outside the nest). Since potential cues vary in their value as indicators, one might expect that, through evolution, only very good cues—those with a high, reliable, and functional informative content—have been retained as decision criteria. In other words, the “intelligence” of a decision criterion results not simply from the use of cues that intrinsically catch a part of the environmental complexity, but also from the selection of the best cue—that is, the one most pertinent for the activity of the ants. Both recruitment strategies described in the previous section are based on such intelligent decision criteria.

As regards scavenging, prey retrievability is a seemingly crude estimator of prey size. Nevertheless, it is a highly functional decision criterion because it integrates information not only about the size, the shape, and the weight of the prey, but also about environmental factors that alter its retrievability. Such factors would include the surface roughness and slope of the soil and the density of the vegetation (Fig. 3A). This decision criterion is also a means for each forager to assess the current force of cooperating carriers and the possible need to recruit additional helpers.

The “desired volume” criterion plays an essential role in the regulation of foraging and in the adjustment of the number of recruiting ants to the productivity profile of aphid colonies (Maillieux, 2001). Monte Carlo simulations based on this simple behavioral rule also predict the existence of an optimum number of foragers that maximizes trail recruitment for a given honeydew production (Fig. 4, see caption

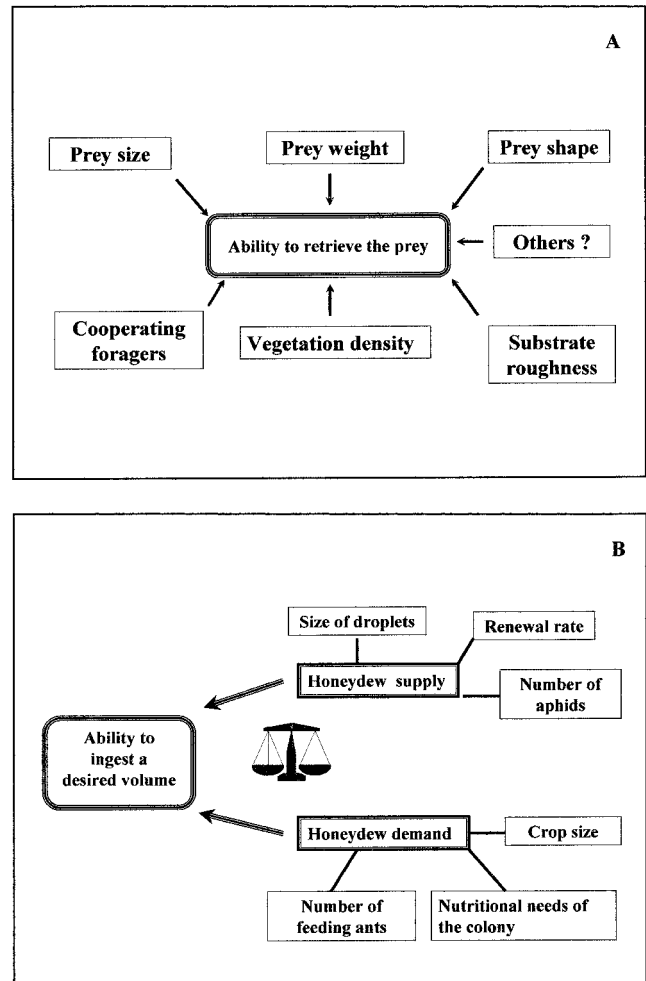


Figure 3. Examples of intelligent decision criteria used by ants to recruit. Such decision criteria automatically integrate multiple parameters from the environment and the colony in the case of prey scavenging (A) and honeydew exploitation (B).

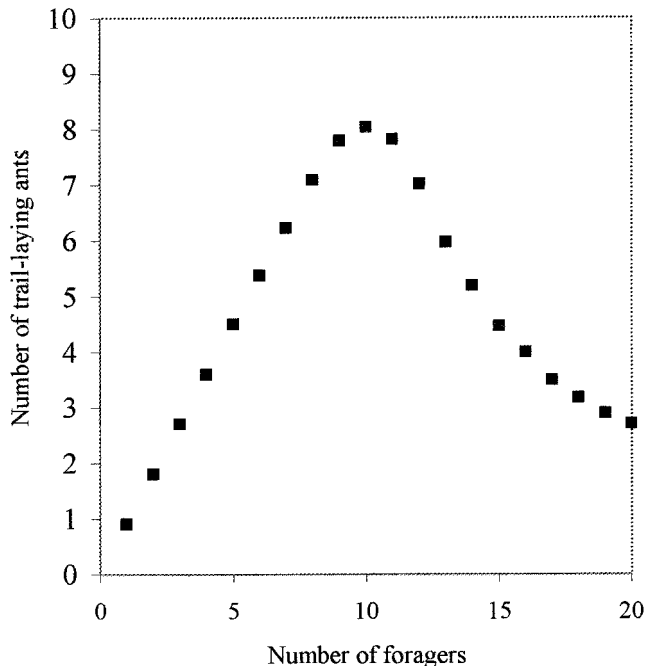


Figure 4. Regulation of the number of trail-laying ants as a function of the number of foragers attending aphids. The curve was drawn for a total production of $10 \mu\text{l}$ honeydew by 400 aphids, each emitting $0.025 \mu\text{l}$ of droplet. Results from 2000 Monte Carlo simulations. After Maillieux, 2001. The model assumes that an ant ingests, per second, a volume $\Delta V = 10^{-2} \mu\text{l}$. The probability that an ant will stop ingesting food and leave a source follows a stimulus-response function described in Maillieux *et al.*, 2000. When one source is exhausted, some ants have to leave it even though they have not reached their desired volume. The probabilities for those “unsatisfied” ants (1) to discover an additional source per unit time is equal to $1/20 \text{ s}^{-1}$ and (2) to leave the foraging area without laying a trail per unit time is equal to $1/85 \text{ s}^{-1}$. Satisfied ants that succeed in ingesting their desired volume lay the same amount of trail pheromone whatever the number of visited sources or the ingested volume.

for details about the model). This can be explained by the decrease in the probability of trail-laying when foragers no longer succeed in ingesting their desired volumes due to temporary depletion of or overcrowding at the food sources. Functionally, it means that the global trail intensity increases with the foraging force as long as the supply of honeydew exceeds the demand of the foragers. Conversely, when the demand of the foragers exceeds the supply of honeydew, fewer workers will lay a trail. Hence, the “desired volume” is another intelligent decision rule that takes into account the balance between supply and demand (Fig. 3B). This simple decision criterion indirectly assesses several environmental factors related to honeydew production, such as the number of aphids and the size or renewal rate of emitted droplets. It also implicitly integrates characteristics of the ant colony, such as its nutritive needs, the number of feeding ants, and the ant species’ body size and its related crop load.

The existence of intelligent decision criteria that func-

tionally integrate multiple parameters should be generic for all insect societies. Concerning honeybees, Seeley (1995) emphasizes the importance of cues that incidentally convey reliable information within the hive. One of these cues that influence recruiting behavior is the time spent by a returning forager searching in the hive for a nestmate willing to receive her load of nectar or water (Lindauer, 1971; Seeley, 1989). Similarly, in social wasps, the queuing delay that a forager experiences waiting to be unloaded by a builder conveys information on the colony’s need for the materials (pulp or water) (Jeanne, 1999). These temporal cues are highly informative by-products of the colony’s collection (supply) and consumption (demand) of resources. It is highly probable that intelligent decision criteria have been selected preferentially among cues, like time-based ones, that intrinsically alter the dynamics of a group response based on amplification processes. (For the impact of time delays on collective patterns in ants, see Goss *et al.*, 1989; Detrain *et al.*, 1999.) Through evolution, the reliance of recruitment modulation on such time parameters might have enhanced their already existing effect on the dynamics and hence on the efficiency of the colony response.

That intelligent decision criteria should also occur outside the context of foraging is suggested by studies in ants on nest emigration (Mallon and Franks, 2000), brood rearing (Cassill and Tschinkel, 1999), nest excavation (Rasse and Deneubourg, 2001), and colony fights (Lumsden and Hölldobler, 1983). As proposed by Seeley (1995) concerning the use of cues in honeybee foraging, information transfer based on intelligent decision criteria may evolve more readily than that involving numerous signals coding for each parameter. Indeed, this communication process involves the tuning of only one or a few adaptive decision rules based on preexisting stimuli.

Contribution of the Environment to the Emergence of Self-Organized Patterns

Environmental factors, such as the distribution and abundance of food resources (see Bernstein 1975; Rissing and Wheeler, 1976; Hölldobler, 1976; Hahn and Maschwitz, 1985), the presence of competitors (see Hölldobler, 1976; Acosta *et al.*, 1995), and the existence of predators (see Nonacs and Dill, 1988), act upon the collective patterns of ant colonies. One can question whether these collective patterns arise through changes in the behavior of the ants or as the direct result of the environment’s properties. Evidence of direct contributions of the environment comes from the diversity of foraging patterns that emerge even though individual ants behave similarly. Franks *et al.* (1991) demonstrate how the distribution and abundance of food acts upon the recruitment dynamics of army ants and contributes to the emergence of species-specific raiding patterns. Colonies of *Eciton hamatum* have a dendritic raiding

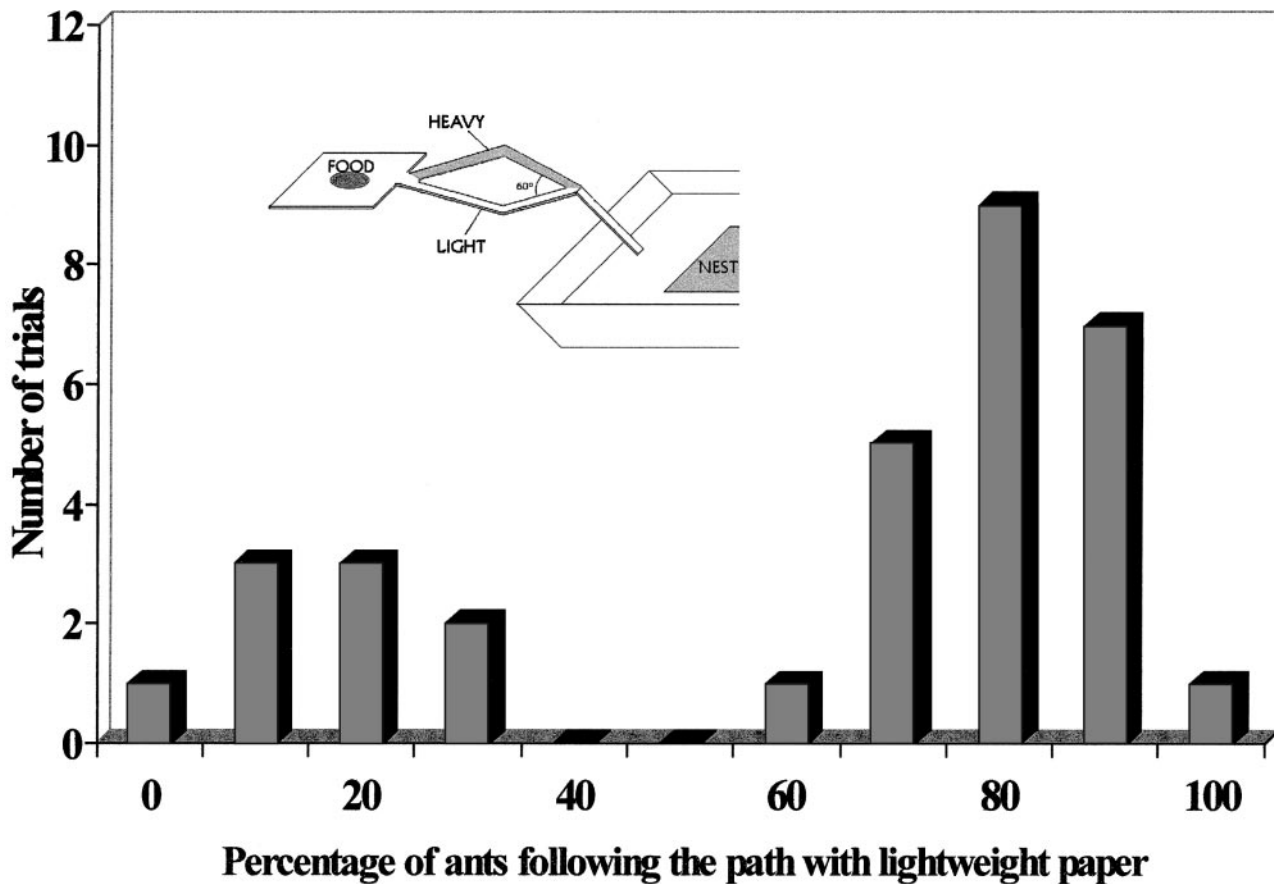


Figure 5. Influence of the substrate on collective choice of a foraging path. The number of trials ($n = 32$) is given as a function of path selection expressed as the percentage of all of the ants traversing the bridge that chose the lightweight paper (x -axis). After Detrain *et al.*, 2001, Fig. 1, © Springer-Verlag. Used with permission.

pattern and attack wasp nests that are rare but large packets of prey. Conversely, colonies of *E. burchelli* have large cohesive raids and prey mainly on common solitary arthropods. One can elicit the splitting of an *E. burchelli* raid into sub-swarms (close to the *E. hamatum* pattern) simply by manipulating the distribution of its prey, gathering them into a few discrete, dense packets. Theoretical studies and empirical knowledge also strongly suggest that an adaptive plasticity and diversity of responses can arise from the same behavioral rule applied in different environments (for a review, see Camazine *et al.*, 2001). Hence, different foraging patterns can arise independently of any modulation of trail recruitment since they can be simple by-products of the biotic environment.

Even the abiotic environment can directly contribute to an ant colony's decision making. Traditionally, the impact of the abiotic environment on foraging patterns has been linked to changes in the behavior of individual ants, as in the case of ambient temperature (Traniello *et al.*, 1984; Marsh, 1985), which influences the activity level, running speed, and searching behavior of individual workers. Here we cast

new light on abiotic factors such as the substrate, which can determine the collective choices of ant colonies without altering or acting as a constraint to behavior at the individual level (Detrain *et al.*, 2001). A nest of *Lasius niger* is given access to a foraging area and a food source via a diamond-shaped bridge, the two branches of which are identical except for the weight of the paper covering their surface. Though paper is an artificial substrate, it allows us to investigate the impact of a chosen abiotic factor on the ants' foraging decisions. After the discovery of the food source, the path covered with the light-weight paper is followed by more than half of foragers in the majority of the trials (72%, $n = 32$, Fig. 5). Surprisingly, this collective preference for one foraging path cannot be linked to any substrate-related change in the individual behaviors of scouting or recruiting ants. Scouts make a similar number of U-turns and walk at the same speed on both paths. Furthermore, after food discovery, similar percentages of ants are engaged in trail-laying and emit the same average numbers of chemical marks whatever the substrate of their foraging path. Clear-cut choices of a foraging path appear to be

driven by the substrate itself independently of any behavioral changes at the individual level. Evidently, physicochemical differences between the two papers alter the accessibility of the trail pheromone to foragers and hence the dynamics of information transfer by chemical trails. Monte Carlo simulations confirm that these differences underlie the ants' collective choices. Note that collective choices are not unanimous (in about 28% of the trials, the heavy substrate was chosen): these "unexpected" choices are signatures of a self-organized process in which "errors" or less likely decisions of the first foragers are amplified by positive feedbacks such as trail recruitment. Hence, the abiotic environment can directly contribute to collective decision-making by determining, through its physicochemical properties, the dynamics of information transfer by chemical trails. This is likely to apply to other information-laden signals such as vibrations produced by stridulating ants, where the recruitment range might depend on the resonance properties of the substrate (Baroni-Urbani *et al.*, 1988). Similarly, for nest construction, the air stream could shape the structures built by termites (regularly spaced pillars or walls) independently of any individual change in building behavior (Bonabeau *et al.*, 1998). Even in vertebrates, some studies suggest that the environment could determine the spatial patterns of animals without altering their individual behavior (see Gérard *et al.*, 2002). Hence, the role of the environment should be reconsidered not simply as a constraint but as a part of the decision-making process, as a shaping agent of collective patterns.

Conclusion

How animals acquire and integrate multiple and complex information from their environment deserves closer analysis. Among social insects, the individual has limited cognitive abilities, assesses only local environmental parameters, and cannot compare its experience to that of all its nestmates. Such limitations of the individual contrast with the diversity of collective responses that efficiently track environmental opportunities and challenges. Self-organization allows insect societies to fill the gap between these two levels of complexity. Global behaviors are generated through competing amplification processes and limiting factors in which individuals follow a few simple decision rules. Rules based on intelligent decision criteria have been selected, since these enable individuals to automatically integrate multiple sources of information that are relevant to a behavioral strategy. The concept of intelligent decision criteria should be more widely investigated for many activities, not only in group-living animals but also in solitary ones, with the aim of understanding how animals cope with the complexity of their world. In the future, new intelligent criteria could be identified mainly among those parameters such as energy or time that are now seen essentially as

optimization criteria (see Roces, 2002). This essay also stresses the direct contribution of the environment to problem-solving. By altering the dynamics of information transfer, some environmental parameters can be responsible, together with simple decision rules, for the emergence of adaptive collective behaviors in self-organized systems as different as insect societies and vertebrate groups.

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