

INVITATION PAPER (C.P. ALEXANDER FUND): FORAGING OF INDIVIDUAL WORKERS IN RELATION TO COLONY STATE IN THE SOCIAL HYMENOPTERA

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Abstract

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Workers of social insects are members of colonies that survive and reproduce together. Therefore, the behavioral activities of individual workers should be integrated with colony state. We here summarize and discuss the relationship between colony state and foraging behavior of individual workers under the provisional assumption that the colony is a unit. We argue that colony state can be described by a number of variables that should relate to fitness components in order to be meaningful. Among the possible candidates, colony population size seems to have an overriding importance in many respects, as shown by its relation to fitness components such as survival probability and reproductive performance. Other important variables include colony demography, i.e. caste or size distributions, nutritional status, or queen number. Each of these variables has been shown to affect fitness components; however, the evidence is rather scanty. We also discuss the evidence that variation in colony state variables relates to variation in individual worker behavior. Nutritional status (i.e. low or high levels of food stores) and colony size have been shown repeatedly to affect individual behavior. However, most of the evidence comes from the honey bee. Some studies suggest that behavioral responses are hierarchically structured. More work needs to be done to investigate the actual mechanisms of integration of individual behavior with colony state. Some knowledge has accumulated about the processes that govern recruitment to food sources. We conclude this review by discussing some concepts and problems for further research. These include the concept of a preferred colony state to which the colony should return after disturbance through the behavioral activities of the workers. Further theoretical elaboration and empirical investigations may help to elucidate whether this concept is useful and necessary. A largely neglected issue concerns the number versus effort problem, i.e. whether individuals should work harder or more workers should be allocated to a task that is in demand. We propose a simple scenario that suggests testable predictions. Finally, we discuss how colony state, individual work load, and the dependence of worker mortality rate on activity level may interact to generate different short-term foraging strategies that workers should adopt.

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Résumé

Chez les insectes sociaux, les ouvrières appartiennent à une colonie où la survie et la reproduction sont des phénomènes collectifs. Les activités comportementales de chacune des ouvrières font donc partie intégrante de l'état de la colonie. La relation entre l'état de la colonie et le comportement de quête de nourriture d'ouvrières particulières est définie et examinée dans le cadre de l'hypothèse selon laquelle la colonie fonctionne comme une unité. Nous croyons que l'état de la colonie peut être décrit par un certain nombre de variables qui n'ont de sens que si elles sont reliées aux composantes du "fitness." Parmi les variables possibles, la taille de la population dans la colonie semble avoir une importance capitale par plusieurs aspects, comme le démontre sa relation avec des composantes telles que la probabilité de survie et le succès de la reproduction. Parmi les autres variables importantes, il faut mentionner la démographie de la colonie, i.e. la répartition selon la caste ou la taille, le statut alimentaire ou le nombre de reines. Chacune de ces variables a un effet sur les composantes du "fitness," mais cependant les preuves en sont plutôt faibles. Nous examinons aussi l'hypothèse d'une relation

entre les fluctuations des variables associées à l'état de la colonie et celles du comportement individuel des ouvrières. Le statut alimentaire (i.e. quantités faibles ou élevées de réserves de nourriture) et la taille de la colonie ont été reconnus à plusieurs reprises comme des facteurs qui affectent le comportement individuel. Cependant, les preuves à l'appui de cette affirmation viennent toutes d'études sur l'Abeille domestique. Certains travaux indiquent que les réactions comportementales dépendent de la hiérarchie sociale. Les mécanismes réels de la contribution des comportements individuels à l'état de la colonie doivent être soumis à des études plus poussées. Les processus qui régissent le recrutement aux sources de nourriture sont mieux connus maintenant. Nous concluons cette synthèse par l'examen de certaines théories et de problèmes qui devront être étudiés plus en détails, en particulier la théorie d'un état optimal que la colonie devrait retrouver après les perturbations entraînées par les activités comportementales des ouvrières. Des spéculations théoriques et des recherches empiriques pourront déterminer si cette théorie est nécessaire, voire utile. La question du nombre-versus-l'effort est toujours fortement négligée; chaque individu devrait-il travailler plus fort ou serait-il préférable que plus d'ouvrières soient affectées à la tâche requise. Nous proposons ici un scénario simple qui suppose des prédictions vérifiables par des tests. Finalement, nous examinons comment l'état de la colonie, la charge de travail de chaque individu et la relation entre le taux de mortalité et la somme de travail peuvent se combiner pour donner lieu à de nouvelles stratégies de recherche de nourriture à court terme que pourraient adopter les ouvrières.

[Traduit par la rédaction]

Introduction

Social insects are an important part of the fauna in many parts of the world. Their habits and ecology vary enormously (see Wilson 1971 for a general introduction; Hölldobler and Wilson 1990 for ants; Michener 1974 for bees; or Ross and Matthews 1990 for wasps), and the activities of social insects affect their environment to a considerable extent. Termites modify tropical soils and facilitate growth of new vegetation (Sylvester-Bradley et al. 1982); in temperate forests, the patrolling and food collection activities of wood ants are vital for the functioning of this ecosystem. Social insects often are commercially important species, either as pests, such as leaf-cutter ants that can devastate plantations in the tropics (Cherret and Peregrine 1976), or as beneficial species, such as honey bees with an estimated increase in bee-pollinated crops valued at \$9.3 billion (Robinson et al. 1989) and annual sales of bee products over \$200 million in the United States alone.

It is the behavioral action of the individual worker, alone or in concert with others, that affects other organisms in the surroundings of a nest. But workers are integrated in subtle ways into their society, so individual activities, even at a distance from the nest and in isolation from other workers, are not independent of the state of the colony itself. Hence, unlike solitary organisms, there is no simple way to relate environmental contingencies to individual actions, for the latter are modulated by the social context.

Social insects form colonies that persist at a site for prolonged periods of time, either as a single nest or a set of nests that exchanges individuals and goods. Colonies vary enormously in size, from several millions in army ants (Wilson 1971) to a few dozens in some ponerine ants (Fresneau 1984). As a rule, the workers must leave the relative safety of the nest to collect food that is used primarily to raise brood. Two different kinds of resources are collected by social Hymenoptera: protein-rich food mainly used for the larvae (e.g. pollen in bees, animal prey in ants) and carbohydrate-rich food mainly used by the adults (nectar and other sugary solutions). Although many different tasks that workers fulfil are important for the functioning of the colony, we concentrate here on foraging behavior, as it is relevant for ecological interactions with other organisms.

Studies of foraging behavior have focused on understanding its short-term economics, i.e. on the time scale of minutes or hours. Economic principles should represent the way

natural selection acts on the traits under scrutiny. For example, the efficiency of leaf collection and processing in the leaf-cutter ant *Atta* is critical for culturing the fungus that serves as the food supply for the colony. Given various physiological constraints, it can be determined which worker size-classes are the most energetically efficient for the various tasks involved in this process. The respective optimal allocation of workers can then be compared with the actual distribution (Wilson 1980a, 1980b). This and a number of other studies (Schmid-Hempel et al. 1985) have demonstrated that it is in principle possible to understand the short-term economics of social insect foraging, and from the aspect of energetics, individual worker behavior is rather efficient. Although it is not usually considered in detail how such behavior actually contributes to the fitness of the colony, theoretical frameworks have been developed to link individual behavior to colony survival and reproductive success (Houston et al. 1988; Franks et al. 1990). However, there have been few empirical studies investigating further the relationship between individual behaviors and colony fitness.

Colony state changes over the course of a season, as colonies grow in size and worker numbers. Reproduction occurs by releasing sexual forms — the gynes and males. There are many variants to the basic life history schedule with annual (many wasps) or perennial (stingless bees, ants) life cycles and with reproduction early (honey bees) or late (bumble bees) in the season. Yet, it is the intensity with which individuals collect resources that profoundly affects colony growth and development. Foraging analyses have led to an increased awareness that benefits are gained by foraging outside the nest, but costs in the form of risk of worker death also are incurred, thus imposing a penalty to colony growth (Porter and Jorgensen 1981; Schmid-Hempel and Schmid-Hempel 1984). Thus, if benefits and costs of foraging depend on activity, individuals should not always work as much as possible. Rather, workers should be expected to vary their level of activity according to the state of the colony.

In this paper, we concentrate on discussing the relationship between individual worker behavior, particularly foraging activity, and colony state in the social Hymenoptera. We present a selective review of what seems presently known about these interrelations and put it into the context of the colony's survival and reproductive success. This work initially has been inspired by our own studies on the honey bee, for which most of the available evidence has been accumulated. We also take the pragmatic view of the colony as a unit of consideration, but do not imply that workers of the colony invariably behave to generate a superorganism in perfect reproductive harmony (Bourke 1988). We will ask what the relevant state parameters might be, and then look at the evidence for individual behavioral changes in response to these state parameters.

The Colony and its State Variables

The notion of an organism's state and the realization that it may affect behavior was introduced to behavioral studies by works such as McFarland and Sibly (1972) or Sibly and McFarland (1973), to be later extended and formalized by McNamara and Houston (1986) or Mangel and Clark (1988). In the social Hymenoptera, colony state may refer to any of a number of colony attributes. It could most generally be thought of as a vector summarizing the current values of all important colony variables, but more practically, in any particular study, it focuses on one or just a few attributes thought to be important in affecting the behavior of interest. These can often be well-defined and measured in experimental procedures.

Characteristics such as worker number, amount of food stored, or amount of brood have often been used as state variables. All of these parameters are likely to be important for colony success, i.e. for the survival and reproduction of the colony and its members. However, there seems to be little data concerning the actual relationship between the value of state variables and colony success. This is not to say that direct consequences are not

to be expected, such as colony failure with heavy food deprivation or heavy worker loss. Yet many interesting phenomena are likely to happen with moderate variation in these state parameters, because this may be the most common situation in the field. We also do not imply that, for example, periods of unusually short food supply might not be major selective events, but merely that on the ecological time scale most variation presumably happens in the moderate range.

Colony Population Size. This is usually meant to indicate the number of adult workers present in a colony at a given time. This state parameter seems to have a universal effect on colony success. For example, the number of workers often affects the production of eggs in ant colonies (Colombel 1972; Smeeton 1982; Brian 1983), or influences body size in workers (Gray 1971; Wood and Tschinkel 1981; Wilson 1983*b*; Porter and Tschinkel 1985*b*; Fowler 1986). Larger worker size usually relates to longer life spans (Franks 1985). Subtle effects of colony population have been investigated by Jeanne (1986) to show that the rate of nest construction in the social wasp *Polybia occidentalis* Olivier is a function of colony population size. This occurs because smooth transfer of nest building materials from one worker to the next affects waiting times and influences the relative timing of the different work cycles for foragers and cell builders. In many cases, the number of sexuals produced by a colony is an increasing function of colony population size up to a point (Michener 1964; Gentry 1974; Pomeroy and Plowright 1982; Elmes and Wardlaw 1982; Seeley 1985; Seeley and Visscher 1985; Lee and Winston 1985*a*; Johnston and Wilson 1985; Müller and Schmid-Hempel 1992).

Similarly, colony population size is important for fitness in the honey bee, *Apis mellifera* L. For example, Lee and Winston (1985*b*) found a positive correlation between swarm population size and both brood production and emergent worker weight in newly founded colonies. In addition, larger colonies invested more workers to the total of swarms, which in turn was associated with increased drone production, a strong component of fitness; but no correlation of colony size with the number of offspring colonies existed (Lee and Winston 1987). Larger swarms also produce more total brood comb and a higher proportion of drone brood (Lee and Winston 1985*a*). The number of swarms that a colony can produce is positively related to the amount of sealed brood at the time when the prime swarm issues (Winston 1979, 1980). Other studies show a positive relationship between colony population size and total brood production (Farrar 1944; Free and Racey 1968; Moeller 1958, 1961; Nelson and Jay 1972; Smirl and Jay 1972). Honey production (an important fitness component as it relates to winter survival) is not necessarily a simple function of colony size (Farrar 1937; Woyke 1984). Winter survival is highest for intermediate colony population sizes, particularly when diseases are present (Jeffree and Allen 1956).

When colony population size is reduced experimentally by removing workers or by natural loss, negative effects on fitness components are observed. These include shorter life spans for the remaining workers coupled with workers starting to forage at younger ages (Winston and Fergusson 1985). However, when spring colonies are reduced in worker numbers, they will recover so that they are equal to controls in adult worker populations, and in honey or pollen storage by the end of the season (Winston et al. 1985). Such astounding resilience to external perturbation seems to be a general characteristic of social insect colonies (unpubl. data).

Worker number also affects colony survival directly. In honey bees, their respective survival probabilities until the next season range from 0 to 8 to 24% (Seeley 1978; Lee 1985; Morales 1986), but the survival rate of established colonies is substantially larger (78% in New York State, Seeley 1978; 45% in Ontario, Morales 1986). The general importance of early survival and development has been reported in a number of independent studies (see reviews in Wilson 1971; Brian 1983). Pleiotropic colony foundation in

TABLE 1. Colony population size (worker numbers) and its relation to components of fitness. Only social insects other than the honey bee have been included. For honey bees, see text

Species	Parameter and relation to fitness	Remarks	Authority
Ants			
<i>Odontomachus haematodes</i>	Egg production by workers depends on worker numbers		Colombel 1972
<i>Pogonomyrmex badius</i>	More reproductives in larger colonies		Gentry 1974
<i>Myrmica</i> spp.	Worker numbers positively correlated with gyne and worker body weights	Queen dominance affected by queen:worker ratio	Elmes 1974
<i>Myrmica rubra</i>	More sexuals with more younger workers as typical for large colonies	More nurses and fewer majors favor gyne production	Brian and Jones 1980
<i>Solenopsis invicta</i>	Worker size increases with colony size		Wood and Tschinkel 1981
<i>Myrmica rubra</i>	Egg production affected by colony size per se, not by worker size		Smeeton 1982
<i>Myrmica sabuleti</i>	Larger colonies produce more sexuals		Elmes and Wardlaw 1982
<i>M. scabrinodis</i>			
<i>Myrmica rubra</i>	Queen has more eggs with more workers, but no more effect above 20 workers	Summarizes the long-term studies on <i>Myrmica</i>	Brian 1983
<i>Leptothorax allardycei</i>	Total brood linearly related to colony size	No reproductivity effect	Cole 1984
<i>Solenopsis invicta</i>	Average size of new workers depends on colony size		Porter and Tschinkel 1985b
<i>S. invicta</i>	Brood production declines with colony size		Porter and Tschinkel 1985a
<i>Camponotus</i> sp.	Mean worker size increases with colony size. Worker and brood number best predictors for production of sexuals	Small colonies about twice as efficient	Fowler 1986
<i>Pheidole dentata</i>	Large colonies produce more sexuals	No relation with CDF*	Johnston and Wilson 1985
Wasps			
<i>Polistes metricus</i>	Multiple foundresses nests produce first workers earlier		Gamboa 1980
<i>Polybia occidentalis</i>	Nest construction faster in large colonies		Jeanne 1986
Bees			
<i>Bombus perplexus</i>	Manipulation of number of first brood affects timing and number of gynes produced	No effect on male production	Pomeroy and Plowright 1982

*CDF = caste distribution function, sensu Oster and Wilson 1978.

wasps (Gibo 1978), bees (Packer 1986), or ants (Bartz and Hölldobler 1982; Rissing and Pollock 1987), which can include cooperation among unrelated individuals (Rissing et al. 1989) during the early colony stages, has been explained in terms of increased survival due to decreased chances of conspecific colony takeovers or loss in territorial disputes (Bartz and Hölldobler 1982), predation and brood-raiding (Tschinkel and Howard 1983), or nest parasitism (*Bombus*, Fisher 1988; *Polistes*, Strassmann et al. 1988).

From this evidence it seems that colony population size is generally an important colony state parameter, as it correlates with several direct components of fitness, including survival and the number of sexuals produced. In addition, large colony population size sometimes correlates with larger worker body size (Table 1) that may add to colony performance, due to prolonged life spans or increased work efficiencies.

Colony Demography. Demography can be characterized by the proportions of different worker size, morph-classes, or castes present in a colony. Oster and Wilson (1978) have discussed the relationship between caste proportions and ecology from a theoretical aspect. How different caste proportions actually translate into fitness differences is not clear (see review in Kolmes 1986; Walker and Stamps 1986; Calabi and Traniello 1989; Schmid-Hempel 1991a, 1991b; Table 2).

The presence of a certain class of individuals, e.g. third-instar larvae (Smeeton 1982) or majors (Brian and Jones 1980) in the ants *Myrmica rubra* L. and *Pheidole bicarinata* Mayr (Wheeler and Nijhout 1983, 1984), can depress the production of new brood and thus can affect colony fitness. Hillesheim et al. (1989) attribute comb construction rate to the ratio of dominant to subordinate workers in colonies of cape honey bees. In some ants, production of soldiers is a function of the number of old workers (Table 2); or in *Iridomyrmex humilis* Mayr the production of males increases with a high worker:larva ratio (Passera et al. 1988; Table 2). The worker:larva ratio has been cited repeatedly as a correlate of, for example, worker body size (Plowright and Jay 1968), productivity (Brian 1953; Elmes and Wardlaw 1982), or as a crucial factor for the onset or extent of reproduction (Röseler 1967; Brian 1980; Yamauchi et al. 1982), but its role and relationship to mature colony size are not clear (Lee and Winston 1985b; Duchateau and Velthuis 1988).

The situation is somewhat different in young colonies. The first workers to emerge in colonies of many social insects are generally smaller ("nanitics") as compared with those emerging from the second and later broods (Oster and Wilson 1978). (Exceptions exist in that some social insect colonies have only one brood before reproduction.) As Porter and Tschinkel (1986; Table 2) have shown for the fire ant *Solenopsis invicta* Buren, having nanitics is adaptive as they are more efficient in producing the next worker generation relative to their weight (the mother's investment). Also, polymorphic colonies of *Solenopsis*, i.e. with different size-classes of workers, produce new workers about 10% more efficiently in energetic terms (Porter and Tschinkel 1985a).

Nutritional Status. Quite obviously, there can be no colony success without food, but the exact effect of food stores on colony survival and reproduction is not well documented. Particularly, quantitative relationships between food stored and colony success are hard to find. In some cases, extra food leads to oversized colonies and presumably to the production of more sexuals (Tschinkel 1988), larger gynes (in *Bombus* with ample pollen supply, Sutcliffe and Plowright 1988), or increased colony growth rates (Southerland 1988). The causal pathways are not always direct, as demonstrated for bumble bees. Depleted nectar stores increase the chances of colony failure, not through starvation but through increased vulnerability to predators and social parasitism as nest defence by the workers is weakened (Cartar and Dill 1991). In harvester ants, there is no clear relationship between survival from one year to the next and foraging activity during the preceding summer (Gordon 1990).

TABLE 2. Demographic parameters and their relation to fitness components

Species	Parameter and relation to fitness	Remarks	Authority
Ants			
<i>Myrmica rubra</i>	More gynes produced with higher proportion of nurses in colony	Nurses (= younger workers) resistant to queen dominance	Brian and Jones 1980
<i>Myrmica rubra</i>	Presence of 3rd-instar larvae depresses egg production		Smeeton 1982
<i>Lasius sakagami</i>	No gynes with high queen densities and/or low worker:queen ratios or high larvae:worker ratios. But more workers and males produced	Highly polygynous species	Yamauchi et al. 1982
<i>Solenopsis invicta</i>	Polymorphic colonies \pm equally productive as monomorphic colonies	Production measured as new brood. Energetic efficiency about 10% higher in polymorphic colonies	Porter and Tschinkel 1985a
<i>Solenopsis invicta</i>	Nanitic workers produce more brood per unit of worker weight		Porter and Tschinkel 1986
<i>Camponotus impressus</i>	No relationship of CDF* with reproductive success		Walker and Stamps 1986
<i>Iridomyrmex humilis</i>	Low worker:larva ratio correlates with reduced male production. No effect on gynes	Protein availability crucial	Passera et al. 1988
<i>Cataglyphis cursor</i>	High nurse:larva ratio relates to more sexuals	Sexualization of normal larvae by nurses, 10–20 days after end of hibernation	Cagniant 1988
<i>Pheidole dentata</i>	No relationship of CDF with reproductive output		Calabi and Traniello 1989
Wasps			
<i>Polistes dominulus</i>	Removal of older larvae increases proportion of longer-lived emerging adults		Theraulaz et al. 1988
Bees			
<i>Apis mellifera</i>	Differences in wax production and foraging between prime and afterswarms related to swarm type	Interpreted as difference in age distributions of swarms	Naumann and Winston 1990
<i>Apis mellifera capensis</i>	Brood comb construction depends on ratio of dominant:subordinate workers	Dominant workers are inefficient nest builders	Hillesheim et al. 1989

*CDF = caste distribution function.

More detailed data are available for the honey bee. Insufficient pollen supply during the larval period leads to shorter life spans and poor development of the glands needed by the worker later in life to fulfil their tasks of brood rearing (Maurizio 1961; Haydak 1972). The kind of pollen fed, i.e. the quality rather than the quantity of food, may also be a source of variation in worker longevity (Schmidt et al. 1987), although these effects await confirmation. A number of factors influence worker emergence weight, including availability of nectar and pollen (Jay 1963). Pollen trapping leads to fewer brood and lower winter survival, and decreased queen longevity (Duff and Furgala 1984). For complex relationships, such as the positive correlation among worker numbers, life span, and dry weight of offspring, the involvement of a nutritional factor can only be loosely inferred (Eischen et al. 1982). Moreover, colonies located far from a food source and thus put at lower food availability will gain less weight per day than those closer (Eckert 1933; Ribbands 1953). There is a good correlation between foraging activity and daily honey production (Marceau et al. 1990). Altogether, typical colonies of honey bees will need some 15–30 kg of pollen and 60–80 kg of nectar each year, of which about 20 kg are consumed overwinter (Seeley 1985). Nutritional status as well as colony population size at the onset of winter are critically important parameters to predict overwinter survival (Seeley 1978; Lee and Winston 1985b; Seeley and Visscher 1985) and hence are important colony state variables.

Colony survival during drought periods is expected to be a function of food storage, and specialized replete (nectar-storing) castes in ants inhabiting arid regions with unpredictable rainfall are well known (Carroll and Janzen 1973). Examples include *Myrmecocystus* (Hölldobler and Wilson 1990) in the southwestern United States, *Prenolepis* in Australia (Wilson 1971), or *Cataglyphis* in North Africa (Schmid-Hempel and Schmid-Hempel 1984).

Other Parameters. Table 3 lists some studies that show an effect of different variables on colony success. One such variable is the presence of more than one queen. Particularly among the ants, many species have more than one functional queen in their colonies (Wilson and Hölldobler 1988). In some studies, no difference in colony performance between mono- or polygynous condition was found (Herbers 1982, 1983); in others, such a difference existed (Vargo and Fletcher 1987). The polygynous condition can be modulated additionally through dominance among the queens and its relation to nest structure (Brian 1988). However, as with queen “quality” (Archer 1981 for *Paravespula vulgaris* L.), the number of queens usually does not vary within colonies but rather between them (if queen elimination early in development is disregarded, e.g. Fletcher and Ross 1985).

Colony state also can be defined by the presence, absence, and severity of parasitic infections. The importance of disease is well known to bee breeders and has obvious effects on colony success (e.g. Morse 1978). For example, infestation by tracheal mites has been shown to lead to colony failure in the honey bee (Royce and Rossignol 1990; Table 3). The microsporidian *Nosema* causes winter losses in the honey bee (Jeffree and Allen 1956); infested queens are more often superseded (Farrar 1947), and infected workers show reduced hoarding behavior (Rinderer and Elliott 1977). Parasitic infection suppresses worker reproduction in the ant *Leptothorax nylanderi* Förster (Salzemann and Plateaux 1987) and in the bumble bee *Bombus terrestris* L. (Shykoff and Schmid-Hempel 1991). Similarly, excess mortality caused by parasitoid flies may lead to loss of reproductive output in *Bombus lucorum* L., particularly if occurring relatively early in the life cycle (Müller and Schmid-Hempel 1992). Because social insects are host to a wide variety of parasitic organisms (Kistner 1982; Hölldobler and Wilson 1990) there should be many subtle effects on fitness that await investigation.

The Usefulness of “Colony State.” As a first approximation, “colony state” is a thinking aid, but its hypothesized components can be real. There are clearly a number of factors

TABLE 3. Miscellaneous parameters of colony state and their relation to fitness components

Species	Parameter and relation to fitness	Remarks	Authority
Ants			
<i>Leptothorax nylanderi</i>	Cestode parasite renders workers sterile. Other workers egg-laying depressed	Species with worker reproduction	Salzemann and Plateaux 1987
<i>Myrmica rubra</i>	Core queens more fecund	Distribution in nest partly regulated by the workers	Brian 1988
<i>Pogonomyrmex badius</i>	Colony mortality independent of colony age (< or > 2 years)	Survival not related to foraging activity in previous year	Gordon 1990
Wasps			
<i>Polistes exclamans</i>	Nest size and level of nest parasitism most important for colony survival	Principal Component Analysis of 11 variables	Strassmann and Thomas 1980
Bees			
<i>Apis mellifera</i>	<i>Nosema</i> infection relates to physiologically older age of workers	Affects age-dependent division of labor, thus perhaps success	Wang and Moeller 1970
<i>Bombus terrestris</i>	Amalgated and requeened colonies grow faster than non-manipulated. No effect on reproductive output	Amalgated colonies contain brood of two colonies	Fisher and Pomeroy 1989
<i>Apis mellifera</i>	Infestation with tracheal mites can be cause of colony failure		Royce and Rossignol 1990
<i>Apis mellifera</i>	Moderate to heavily infested colonies lose significant proportion of workers over winter (tracheal mites)	In heavily infested colonies, overwinter performance correlated with parasite load	Eischen 1987
<i>Apis mellifera</i>	Infestation with tracheal mites reduces honey production	Infestation likely to increase forager mortality	Eischen et al. 1989
<i>Apis mellifera</i>	Infestation with tracheal mites reduces colony growth		Furgala et al. 1989 Otis et al. 1988
<i>Bombus lucorum</i>	Colony size early in life cycle more important than late	Effect for males but not for gynes	Müller and Schmid-Hempel 1992

that can be used as reliable predictors for future colony success. Among them, colony size, i.e. the number of workers present at any one time, most notably at time of colony maturity, stands out. Often colony population size is of overriding importance even if more than one parameter is taken into account (Strassmann and Thomas 1980; Fowler 1986). Clearly, colony population size summarizes a multitude of other interrelationships that affect colony success and can thus rightly be regarded as a centrally important state variable.

Nutritional status of the colony, i.e. the amount of food stored or accumulated in the workers (e.g. the honey pot workers in ants), is likely another useful state variable. Much more work needs to be done to gain a more precise understanding of how a particular nutritional state relates to colony fitness. In contrast, the importance of a certain demographic profile seems less clear, although it has been demonstrated in several cases that demographics affect the production of new workers (Porter and Tschinkel 1985*a*, 1986). How different proportions of castes affect reproductive performance is also not clear. But caste structures are slowly restored after disturbance, which hints to some functional value (Gentry 1974; Herbers 1980; Wilson 1983*a*; Fowler 1985, 1986; Porter and Tschinkel 1985*b*; Johnston and Wilson 1985; Winston et al. 1985). In a well-investigated case, the rebound in the distribution of worker body sizes after experimental removal of colony members was a function of colony size rather than colony age (Wilson 1983*b*). Parasitic infestation is another component of colony state, but little is known about the influence of this factor in most social insects apart from the honey bee (see Morse 1978). In the bumble bee *B. terrestris* L., infection by trypanosomes alters the age-distribution of workers in a colony and reduces colony growth during the early part of the life cycle (Shykoff and Schmid-Hempel 1991). In ants, fungus infections have been reported for various species, but they seem to have a minor impact on colony demography, presumably due to antibiotic secretions produced by exocrine organs that keep infections under control (Hölldobler and Wilson 1990).

Thus, there can be little doubt that different conditions of the colony bear on its future success, just as is the case in any other organism. The relationships may not be as clear in social insects, because social insect colonies show an astonishing degree of resilience against external perturbations, and a large degree of intercolony variability in almost any parameter that has been looked at (unpubl. data). Nevertheless, we can predict that changes in colony state will be reflected in a change in individual behaviors, if the latter are selected through their effects on colony success (Hamilton 1964).

Colony State and Behavioral Changes

A number of colony state variables relate to colony survival and reproduction. Hence, is there a change in the behavioral activities of individuals when such variables change? Experimental manipulation of several colony state variables has demonstrated a dependence of individual behaviors (Table 4).

In particular, variation in colony population size seems important in affecting what individual foragers do (Tables 4, 5). For example, Wilson (1984) removed a fraction of the workers from colonies of *Pheidole*, resulting in increased activity of the remaining workers. This finding also has been reported for the honey bee (Terada et al. 1975; Winston and Fergusson 1985; Wolf and Schmid-Hempel 1990). Colony size may also affect more specific behaviors, such as the proneness to risky tasks like foraging, in the social wasp *Polistes exclamans* Viereck (Strassmann 1985), and colony defence (Collins and Kubasek 1982, with a negative correlation between colony size and number of stings on a target, although the evidence is not clear-cut). Oster and Wilson (1978) indicate that, generally, the workers from young colonies are more timid in their behaviors. There is also a negative correlation between average colony size and the time spent inactive, or the frequency of self-grooming across different ant species (Schmid-Hempel 1990). The latter behaviors are assumed to benefit the individual worker rather than the colony as a whole. This pattern

TABLE 4. Individual behavioral response to variation in colony state variables. For studies with the honey bee, see Table 5

Species	State variable	Finding	Authority
Ants			
<i>Solenopsis invicta</i> (E)*	Food	Colony saturated with food alters diet choice of workers	Glunn et al. 1981
<i>Odontomachus affinis</i> (O)*	Colony age	Relative time budgets of worker activities change with colony age	Brandao 1983
<i>Atta cephalotes</i> (E)	Demography	Removal of medium-sized workers does not affect overall foraging rate as others join in	Wilson 1983a, 1983b
<i>Pheidole</i> spp. (E)	Colony size	After worker removal remaining workers become more active	Wilson 1984
<i>Polyergus breviceps</i> (E)	Food	In saturated colonies the frequency of slave raids is reduced	Topoff 1985
<i>Pogonomyrmex barbatus</i> (E)	Work allocation	Obstruction of one activity changes work levels in all other activities	Gordon 1986
<i>Pogonomyrmex barbatus</i> (O)	Colony age	Foragers from younger colonies (< 2 years) more persistent in re-searching food sites	Gordon 1989
<i>Pogonomyrmex californicus</i> (E)	Food	Starvation of colony has no effect on choice of seed size	Bailey and Polis 1987
<i>Aphaenogaster subterraneum</i> (E)	Queen-rightness	Activity of young workers is regulated by presence of queen	Agboga 1989
Wasps			
<i>Polistes metricus</i> (E)	Demography	Removal of older workers increased foraging rate and efficiency (loads per trip). Queens, total time outside nest not affected	Dew and Michener 1981
<i>Polistes fuscatus</i> (E)	Queen-rightness	Queen removal depresses worker activity and synchronization. Queen as central pace maker	Reeve and Gamboa 1983
<i>Polistes fuscatus</i> (E)	Queen-rightness	Presence of queen stimulates foraging activity	Reeve and Gamboa 1987
<i>Polistes exclamans</i> (O)	Colony size	Workers do fewer risky tasks with more females present	Strassmann 1985
Bees			
<i>Bombus occidentalis</i> (E)	Food	Workers prefer variable patch of flowers when colony nectar stores are depleted	Cartar and Dill 1990b
<i>Bombus</i> spp. (E)	Food	Foraging strategy becomes less conservative when colony nectar stores are depleted (i.e. more risk-prone, more energy spending)	Cartar and Dill 1990a

*E = experimental study, O = observational study.

TABLE 5. Individual behavioral responses to colony state variables in the honey bee (*Apis mellifera*)

State variable	Finding	Authority
Pollen store (E)*	Adding pollen reduces pollen foraging activity. Removing pollen increases pollen foraging activity	Free 1967 Barker 1971 Moeller 1972
Queen presence (E)	Queen presence (via odors) stimulates nectar collection	Fewell et al. 1991
Colony size (O)*	Workers from small colonies have shorter life spans, presumably because of higher foraging activity	Jaycox 1970a, 1970b Terrada et al. 1975
Nectar store (E)	Empty comb increases nectar foraging activity	Rinderer 1981
Nectar store (E)	Removal of nectar leads to more and more intense foraging activity, i.e. longer trips	Rinderer 1982
Wax (E)	Removal of wax induces workers to have more locomotory activity, more comb-building, and more wax work at sealed honey cells	Kolmes 1985
Worker numbers (E)	Worker loss leads to earlier foraging ages of workers	Winston and Fegusson 1985
Wax (E)	Massive wax deprivation results in earlier onset of foraging age and increased comb-building activity. Moderate deprivation does not affect foraging	Ferguson and Winston 1988
Parasite load (tracheal mites) (O)	Infested workers not different in frequency of trips, trip times, pollen collection, survivorship, or nectar loads	Gary and Page 1989
Colony size (E)	Workers from larger colonies visit more flowers per trip but have shorter handling times. Tested on artificial flowers with set nectar volume and quality	Wolf and Schmid-Hempel 1990
Colony size (E)	Workers from smaller colonies bring back smaller nectar loads and stay outside shorter length of time	Eckert 1990
Pollen (E)	Increased amount of eggs and larvae increases pollen foraging	Eckert 1990
Pollen (E)	Workers from pollen-deprived colonies bring back larger pollen loads. Higher proportion of foragers collect pollen. Loads contain more total nitrogen	Fewell and Winston 1992

*E = experimental study, O = observational study.

would relate to some intrinsic species characteristic thought to have been established over evolutionary time rather than variation over the ecological time, which is of prime interest here.

Some of the other state variables discussed above, such as nutritional status, also have been demonstrated to affect individual behaviors. Saturated colonies of the slave-making ant *Polyergus breviceps* Emery, i.e. colonies fed in excess, will reduce the frequency of slave raids (Topoff 1985). Similarly, saturated colonies of *Solenopsis invicta* Buren show altered preferences for food items (Glunn et al. 1981). Hence, the observed behavioral changes are consistent with expectations from simple models of foraging behavior (see Stephens and Krebs 1986), as individuals often will become less active or more selective if the colony has a better nutritional status (Free 1967; Barker 1971; Rinderer 1981, 1982; Glunn et al. 1981; Topoff 1985; Cartar and Dill 1990a, 1990b).

There also is a substantial body of evidence demonstrating that by depriving the colony of a particular resource, e.g. nectar or pollen in bees, the collection of the commodity in short supply is activated (see Table 5). Most studies give no indication of whether the individual behavior has changed in addition to an increase in the number or proportion of workers allocated to this task (but see Rinderer 1982; Wolf and Schmid-Hempel 1990; Fewell et al. 1991; Fewell and Winston 1992). Because pollen is needed to feed larvae, the presence of large amounts of brood relative to pollen supply can increase pollen foraging activity in bees (e.g. in bumble bees, Free 1955). This also seems to occur in animal prey raids by army ants (Schneirla 1944).

The presence or absence of the queen is important for individual activities (Free 1967; Jaycox 1970a; Agboga 1989). These observations have led to the hypothesis that the queen may act as a kind of central pacemaker for the colony (Schneirla 1944; Reeve and Gamboa 1983, 1987). In fact, bursts of activity that periodically spread throughout a colony may be characteristic of many social insect species (Franks and Bryant 1987) and could be generated by some autocatalytic processes (Goss and Deneubourg 1989).

In the honey bee, a wealth of information exists about how the probability of workers performing particular tasks changes with colony condition (Table 5). In the ontogenetic profile, virtually every task can be shifted by a change in conditions such as colony size, food supply, and so forth (see reviews in Seeley 1985; Winston 1987). For example, wax deprivation not only results in workers showing more activities related to comb-building, but they also forage at younger ages and have larger wax scales (Winston and Fergusson 1985). Nectar foraging activity is affected by the amount of empty comb (Jaycox 1970a; 1970b; Rinderer and Baxter 1978; Rinderer 1981), and pollen foraging is influenced by the amount of brood present (sealed and unsealed) (Filmer 1932; Todd and Reed 1970; Barker 1971; Al-Tikrity et al. 1972; Free 1967; Hellmich and Rothenbuhler 1986; Eckert 1990) and probably by feeding carbohydrates (Barker 1971; Free 1965; but see Free 1967) or pollen (Moeller 1972). However, in almost all of these studies, the change "within" individuals is not reported, i.e. it is not known whether individuals simply forage more frequently or whether they also change their behavior in other ways, e.g. by becoming more selective or more risk-prone (see Real 1981). The few exceptions will be discussed below.

As stated before, colony failure in honey bees can result from infestation with tracheal mites (Royce and Rossignol 1990), but rather surprisingly, infested workers do not change their foraging behavior (Gary and Page 1989). Various pathogens can also lead to colony failure (e.g. Morse 1978). However, effects of parasitic infestation, although common, may be subtle, as in colonies of the bumble bee *Bombus terrestris* L. that are infested by the trypanosome *Crithidia bombi* Lipa and Triggiani 1980. In this case, workers become more "social," and defer their own egg-laying thus reducing the queen-worker conflict over reproduction (Shykoff and Schmid-Hempel 1991).

An important characteristic of social insects is documented by the work of Gordon (1986, 1987, 1989, 1990). In a series of experiments, she showed that perturbation of one activity (e.g. foraging) invariably affects other activities (e.g. nest maintenance). Moreover, activities can be ordered according to priorities. In the harvester ant *Pogonomyrmex*, foraging has very high priority and is only mildly affected by obstruction of other activities (Gordon 1986). Thus, flexibility on the individual level combined with hierarchical task evaluation adds further complexity and may mask any direct link between colony state and individual behavior.

In some of the studies mentioned above and in Tables 4 and 5, the behavior of individual workers has been investigated more closely, again mostly in honey bees. For example, removing nectar from colonies leads to intensified foraging, i.e. longer trip durations (Rinderer 1982). Similarly, in manipulating colony size, Wolf and Schmid-Hempel (1990) found that workers from experimentally reduced colonies visit somewhat fewer flowers and stay longer on each one of them than do workers from normal-sized colonies. This difference disappeared over the course of the summer as colony sizes became similar. Similarly, the average worker from a small colony delivered smaller nectar loads and made shorter and fewer foraging trips per day than foragers from larger colonies (Eckert 1990). Simultaneously, the proportion of workers allocated to pollen collection was larger in small colonies. Fewell et al. (1991) demonstrated an effect of colony size on load sizes, sugar contents of loads, and various other foraging parameters for workers of the honey bee tested at distant food patches. Fewell and Winston (1992) either removed or supplemented colonies with pollen. As a result, workers from colonies with poor pollen supply increased the rate of foraging trips, shortened trip length, delivered heavier pollen loads to the nest, and collected pollen with smaller nitrogen content but overall larger nitrogen delivery (mg per load) as compared with their supplemented counterparts.

In addition to these well-documented cases in the honey bee, the nutritional status of bumble bee colonies has been shown to alter the individual behavior of the workers at distant food sources. Bees from nectar-deprived colonies use strategies that have relatively large energy costs (Cartar and Dill 1990a). Moreover, they prefer flowers with variable rewards over those with constant rewards (Cartar and Dill 1990b) and are less sensitive to the presence of a simulated predator (Cartar 1991).

Mechanisms of Integration

As discussed above, individual activities are integrated into the society's needs and modulated according to environmental contingencies. However, this does not yet answer the question of how this integration is achieved. In the context of this paper, how workers assess colony state and adjust their behavior accordingly are the most penetrating questions.

Although a considerable body of literature has accumulated on the general topic of how workers are integrated into the society, most studies have been concerned with the process of recruitment of nestmates to newly discovered food sources. Recruitment is an obvious component of integrating the activity of different individuals to the same end. The work of Seeley (1986, 1989) on the honey bee is particularly relevant here (see also reviews in Brian 1983, or Hölldobler and Wilson 1990). Seeley found that returning honey bees could assess the value of their load relative to the colony's needs through variation in unloading time. Hence, individual assessment through cues provided by others (receiver bees) in combination with internal calibration adjusts recruitment responses.

Some studies report an inhibiting effect of certain larval instars or worker classes on the production of new workers (e.g. with third-instar larvae of *Myrmica rubra* L., Smeeton 1982). At least some of this effect seems to be due to the presence of pheromones. Differential response thresholds among worker age or size groups for the dominating influence of the queen may then have consequences for the overall colony effect, because the latter would be a function of the demography of the worker population (e.g. in *Myrmica rubra*,

Brian and Jones 1980). In many species of social insects there are several overlapping generations of larval instars present at any time, such that the relative contributions of each one are important. Moreover, it is often the queen herself that acts as a regulator of colony and individual activities, as in *Polistes exclamans* Viereck (Reeve and Gamboa 1983).

A honey bee queen mandibular pheromone inhibits workers from rearing new queens (Winston et al. 1989, 1990, 1991), but also stimulates pollen foraging at the same time (Higo et al. 1992). In fact, the latter study shows that not only are more foragers likely to collect pollen, but they bring back larger pollen loads. The effect is strong in young, growing colonies that need lots of pollen but not so in older more established colonies. A brood pheromone deposited on the comb itself also stimulates pollen foraging (Higo et al. 1992). Thus, pheromones originating from the queen play an important role in modulating the overall activity level of the workers. The magnitudes of the effects depend both on status of the colony and environmental conditions. Generally, pheromones are among the most important mediators of colony state (see review in Free 1987).

Trophallaxis has long been suspected to play an important role in the cohesiveness of the insect society. The intensity of trophallaxis can be readily demonstrated by showing that marked food is spread within a short time among all the workers of a colony (Nixon and Ribbands 1951 in honey bees; Wilson and Eisner 1957 in ants). Such exchange could be important to modulate individual activities and affect the schedule of age-dependent polyethism (Free 1967; Korst and Velthuis 1982). In species not regularly engaging in trophallaxis, individual inspection could provide each worker with information about the colony's state. This could be the case in insects like primitively eusocial bumble bees. However, Pendrel and Plowright (1981) found no evidence for a feedback on pollen foraging activity by inspection of larvae.

On a more general level, Wilson and Hölldobler (1988) suggest that insect societies are organized in dense heterarchies, involving redundant chains of activities organized in series or parallel (see also Oster and Wilson 1978; Herbers 1981; Gordon 1989). Although this could explain much of the observed resilience of the colony as well as the seemingly erratic performance of individuals, there is as yet no direct indication of how colony state should affect individual behavior under these conditions. In fact, the knowledge about integrative mechanisms is as yet rather sparse and almost exclusively restricted to the study of the honey bee.

About Some Concepts for Further Research

The Preferred State. In classical ethological studies, state is assumed to control behavior. For example, thirst activates water-seeking behavior. As McFarland (1971) pointed out, however, it is more convenient to think about a feedback loop, in which activated behavior in turn alters state. In guiding future research we therefore need to be able to describe both colony state and individual behavior to understand how they influence each other. At this point, it is necessary to emphasize that there are a number of studies that model the development and population dynamics of social insect colonies (e.g. Brian et al. 1981). We have not specifically dealt with them, as such models are descriptive in the sense of simulating colony-level dynamical patterns by implementing a hypothesized pattern or mechanism of birth, death, or resource collection. Here, we are more concerned with models that would eventually allow us to make predictions on a priori grounds, i.e. by making reference to adaptive value.

Let us assume that the state of a colony can be described by a state vector $\mathbf{x} = \mathbf{x}(t) = \{x_1(t), x_2(t), \dots\}$. Such state vectors do not really exist, but are fictitious variables to help us understand our observations. This has to be separated from the fact that variation in sensible parameters such as colony size, demographic profile, or food stores correlates with variation in further colony survival and reproductive success. We further assume that it is possible to find a state, $\mathbf{x}^*(t)$, for any time t , that if adopted by the colony would result

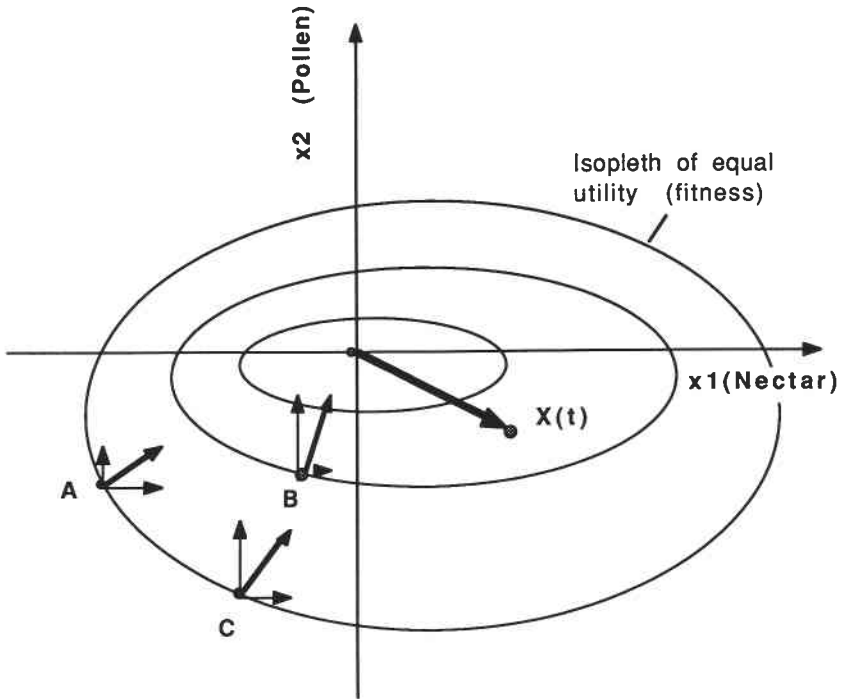


FIG. 1. The colony state space. The two axes represent the deviation in nectar (x_1) and pollen (x_2) stored or availability within the colony (as an example for two components of state). The best state (i.e. availability of the resources) at this moment in time is at the origin. Deviations are associated with a fitness loss, e.g. the deviation given by state $X(t)$, as indicated by isopleths of equal utility. Allocation of workers to behavioral actions should reduce the deficit and bring the colony status back to the origin. Hence, the components of the vectors at deficits A, B, or C (here defined by the tangent to the isopleths) may indicate the relative efforts that should be invested in either collecting pollen or nectar.

in maximum expected lifetime fitness. That such preferred states do exist could be inferred from the fact that colonies of social insects usually rebound after disturbances. This is true, for example, for short-term behavioral actions (Gordon 1989), as well as for the proportions of different age- or size-classes of workers (Herbers 1980; Johnston and Wilson 1985; Winston et al. 1985). By definition, any deviation from x^* carries with it a loss in fitness. The activated behavioral systems work to move the colony back to its preferred state. A similar framework has been formulated by McNamara and Houston (1986) where maximum expected fitness is achieved with minimizing, at any moment in time, a quantity called the canonical cost that describes the cost of deviating from the best trajectory.

Figure 1 provides a visual representation of the idea, showing two components x_1 , x_2 of the state vector (viz. amount of retrieved nectar and pollen), assigned such that the origin is identical to the preferred state (at a given moment). Any perturbation of the colony state, caused either by sudden events such as predation or removal of workers or by chronically scarce food supply, would mean that colony state is removed from the origin by some distance. The distance from the origin is an image of the (canonical) cost that the colony pays in terms of reproductive success for its deviation.

The cost is not isometric around the origin because in Figure 1 a unit deviation in x_1 is more expensive in terms of lost future reproduction than is a unit deviation in x_2 . The isopleths represent deviations of equal cost though. Note that these considerations are

similar to discussions of allocation of individual action to competing needs that occupy the final common path in the behavioral action system (Sibly and MacFarland 1974). However, in social insects actions can take place in parallel rather than in series. Therefore, the final common path is not as limiting to action as in solitary organisms, and both components could be reduced simultaneously by allocating workers to the two tasks (i.e. reducing deficits x_1 and x_2 in Fig. 1).

Houston et al. (1988) predicted that workers from small colonies of honey bees should work harder to collect nectar as compared with workers from large colonies, because of the greater value of the resource for growing colonies. Wolf and Schmid-Hempel (1990) tested this idea, but found the reverse pattern. The colony state concept (Fig. 1) provides a way to understand this apparent contradiction: In the setup used by Wolf and Schmid-Hempel (1990) colony population size was reduced experimentally to increase the need for nectar (state variable x_1). However, later observations suggested that this manipulation increased the need for pollen (state variable x_2) even more so. (In Fig. 1, the experimental manipulation was intended to move the colony from the origin to state A; in reality, however, it was moved to state C.) Hence, the colony invested more into pollen collection but relatively less into nectar foraging. But, as expected from the model of Houston et al. (1988), the total effort into foraging increased (a result that later was corroborated by Eckert 1990 and Fewell and Winston 1992). This finding can be generalized for other situations where changing one parameter simultaneously affects more than one "hidden" state variable x_i . A net result would actually be the kind of interrelated changes in behavioral actions documented by Gordon (1986, 1987).

Because we deal with a dynamic process unfolding over the seasonal cycle of a colony, it does not necessarily mean that the deficit should be reduced on the shortest route to the origin in Figure 1. However, we could define the origin and the isopleths in a way that would actually reflect the dynamics of these costs over the lifetime process. If this was already accurately represented in Figure 1, the graph would tell us that, depending on the relative magnitudes of the two deficit values, the effort that should be invested for reducing deficit x_1 versus deficit x_2 may be quite different for different situations even at equal fitness costs (i.e. on the same isopleth). Note also that a hill-climbing procedure to find the best trajectory for the deficit reduction is not necessarily a good guide for experimentation but merely an aid in thinking about the problem.

There may nevertheless be ways in which, for a particular situation, actual values for the isopleths could be gained. For example, it would be possible to measure colony fitness for a set of conditions encountered throughout the season. This would allow fitness costs to be plotted as a function of colony state for a variety of combinations. Given the many possibilities and the time frame, this task is rather daunting. Alternatively, such curves may be gained through optimization procedures such as dynamic programming (Mangel and Clark 1988), by numerically simulating the various courses of actions and relating them to fitness payoffs, or by employing techniques of genetic algorithms (Goldberg 1989). Furthermore, techniques relating to the analysis of neural networks and path coefficient analysis may be applied.

The Number-versus-Effort Problem. We have discussed the possibility that colonies should invest efforts into regaining their preferred state, e.g. to replenish a resource in great demand. This does not yet define how such an effort may be distributed. In social insects either more workers will do the same thing, or each worker will increase its own individual effort. We refer to this distinction as the number-versus-effort problem.

As the previous discussion has shown, there are good reasons to suggest that individual workers can alter their individual efforts in response to colony state (Wolf and Schmid-Hempel 1990; Fewell and Winston 1992). Similarly, it has long been known that more workers can be recruited to do the same job, as for example with an increase in

pollen collection upon demand (Free 1967). These studies also have demonstrated that both worker number and their individual efforts vary at the same time, often with more workers, and each one working harder at the same job (see also Rinderer 1982). Fergusson and Winston (1988) have demonstrated an "effort" response to moderate deprivation of wax in the honey bee, but an "effort-plus-number" response to heavy deprivation.

In the theoretical analysis of these problems, however, number and effort usually have been kept apart. For example, in Taylor's (1977, 1978) classical studies on recruitment in the ants *Pogonomyrmex* and *Solenopsis* the model workers were forced to carry a unit load of food back to the nest, thus implementing a constant work effort by the individuals while permitting variation of worker numbers. Similarly, in the analysis of individual efforts (Schmid-Hempel et al. 1985), variation of worker numbers is not an issue, and individuals are allowed to vary their work load in accordance with environmental conditions and colony state. Work load is defined here in a very general sense, meaning the effort individuals invest into a particular activity measured as, for example, the amount of time spent foraging, the size of the load carried back to the nest, or the propensity to defend a nest against a predator.

It therefore seems reasonable to ask under which conditions it would pay to recruit more workers (the number response) rather than having each forager work harder (the effort response). To gain an understanding, let us assume that, in general, large colonies have higher fitness, particularly a large worker population at time of reproduction. With this assumption, Houston et al. (1988) argued that maximization of the colony population at the end of a cycle translates into maximization of the instantaneous rate of colony growth, i.e. the difference between birth rate and mortality rate of workers in the colony, at any time during colony development. This scenario, though simplified, is warranted on many grounds. As was discussed before, the number of reproductives that can be produced, as well as a number of other fitness-relevant parameters, generally show a positive correlation with colony size at least up to a point (cf. Table 1). On the other hand, many complicating factors are not included, such as sex allocation and protandry (Bulmer 1983) or the effect of temporally varying environments.

But let us assume that in this simple scenario, the cost-benefit structure of working to collect a resource looks like the graphs depicted in Figure 2. Hence, with increasing individual work effort, f , the rate of return for the colony, $b = b(f)$, which is directly related to the birth rate of new workers as $c \cdot b(f)$, where $c =$ a constant, increases up to a point, before tapering off and declining. Similarly, the cost function (here identical to the mortality rate of workers, μ) increases monotonically with effort f , $\mu = \mu(f)$. Mutual interference of workers and start-up costs (e.g. the recruitment process) are neglected here. If n workers are allocated, each working at level f in a particular task, then the growth rate, R , achieved by the colony at that moment in its life cycle is given by:

$$R = n \cdot [c \cdot b(f) - \mu(f)]. \quad [1]$$

R is to be maximized by simultaneously varying n and f with our argument above. Hence, if each worker decides to change work load by a small amount ∂f , the change in R is:

$$\partial R / \partial f = n \cdot [c \cdot db(f) / df - d\mu(f) / df]. \quad [2]$$

On the other hand, if the number of workers at effort f is varied then the resulting growth increment is (worker number is taken as a continuous variable):

$$\partial R / \partial n = c \cdot b(f) - \mu(f). \quad [3]$$

Hence, it would pay to send out more workers rather than to let each individual work more if:

$$[c \cdot b(f) - \mu(f)] / n > [c \cdot db(f) / df - d\mu(f) / df] \quad [4]$$

and the opposite is predicted if the condition in Eq. [4] is not met. The righthand side of

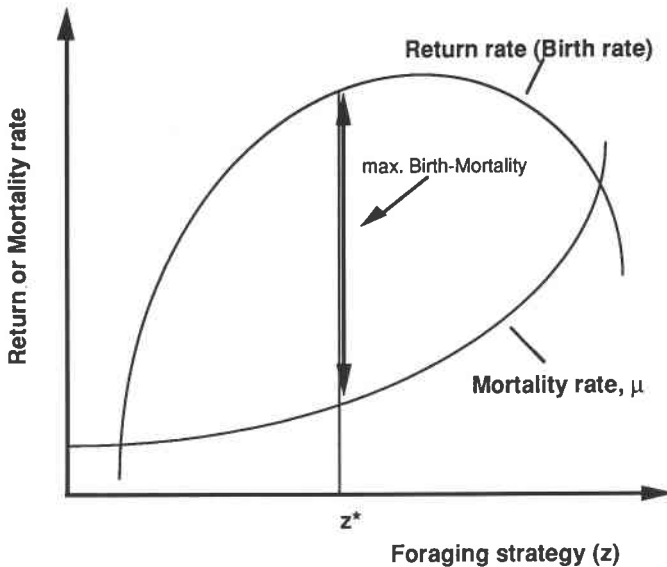


FIG. 2. A simple relationship between foraging strategy (z), return rate per worker (proportional to birth rate, b , of workers), and mortality rate, μ . The strategy maximizing colony growth rate is indicated by z^* (after Houston et al. 1988).

Eq. [4] describes the extra benefit for the colony if foragers work harder (or more generally, the variation in colony gain with variation in work load around f). If this extra benefit is small, recruitment may pay. But as n increases, this condition becomes less likely to hold. However, if variation in f has a large effect (i.e. the righthand side is large), working harder should be favored. As work load increases, the threshold for recruiting more foragers will be reached (as the condition in Eq. [4] is fulfilled), which in turn (by then adding a worker to quantity n) will again favor harder work. The net process is that work effort and numbers will increase together.

It is clear from the formulation of this model in Eqs. [2] and [3] that this process must stop at some value of f^* , when the increment of Eq. [2] becomes zero. However, ever more workers up to $n \rightarrow \infty$ can be added before the numerical response no longer pays. Obviously then, this model does omit a number of important constraints. For example, mutual interference of workers, which can be modeled by letting $b = b(f, n)$ be a function of both work effort and number of workers, start-up costs, or a limited number of workers available for foraging are important additions for any reasonable analysis. With the interference amendment, Eq. [3] will read:

$$\partial R / \partial n = c \cdot [b(f, n) + n \cdot db(f, n) / dn] - \mu(f) \quad [3a]$$

where interference implies $db(f, n) / dn < 0$. The process will stop when increments, Eqs. [2] and [3a], become zero. This scenario is visualized in Figure 3, showing that at this point many foragers will have been recruited, but each one is working less than they would if fewer workers were involved in this task.

Individual Foraging Strategy and Colony Integration. The integration of individual behavior with colony state has further repercussions for the analysis of individual foraging strategies. Here, the approach is "bottom-up" by focusing on foraging currencies that would accurately predict short-term foraging behavior, and then asking how this may be a result of integration within a colony.

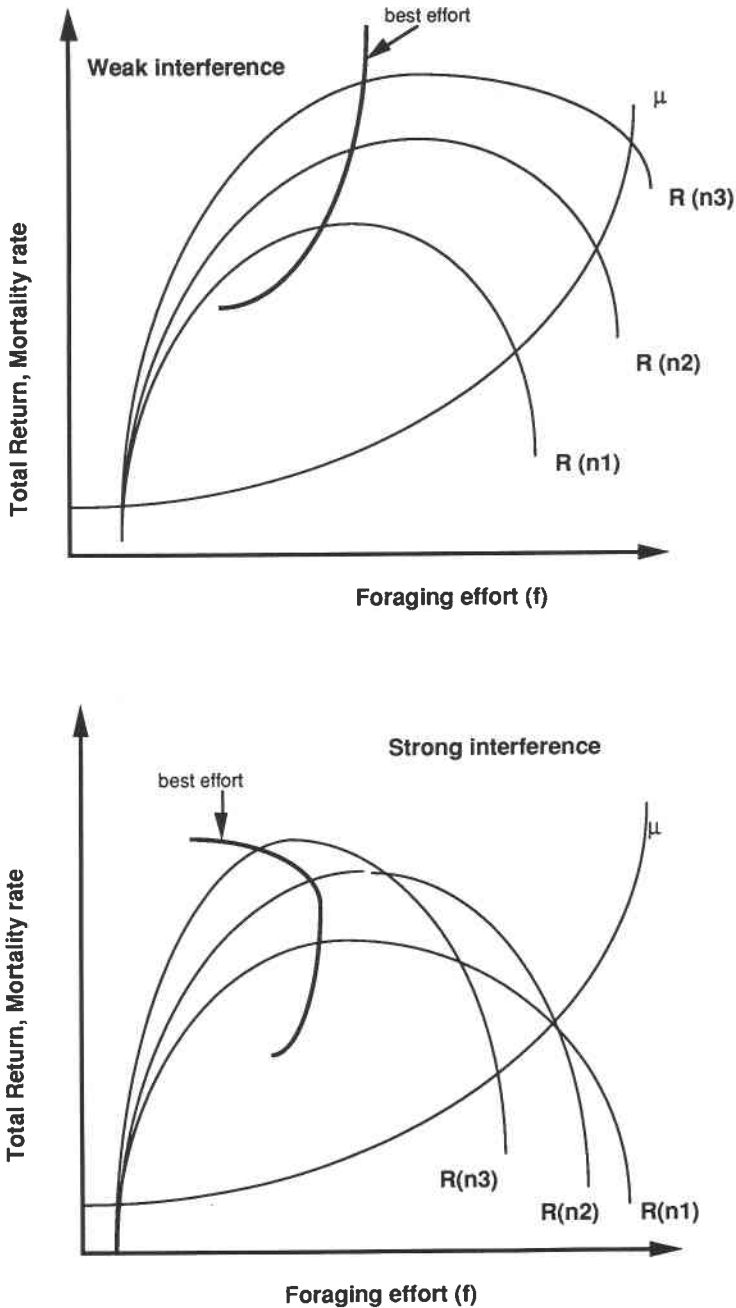


FIG. 3. Total return rate for the colony if n_1 , n_2 , or n_3 workers ($n_3 > n_2 > n_1$) are allocated to foraging, each working at effort f . The heavy line indicates how work effort per worker (abscissa) varies with number of workers allocated to the task if (a) mutual interference of the workers is weak or absent, (b) mutual interference is strong. Interference affects return rate; total mortality scaled appropriately.

The economics of foraging behavior has often been studied in evolutionary biology as an example of adaptive traits (Parker and Maynard Smith 1990). The analysis proceeds by formulating models that incorporate a goal function serving as a fitness token. Foraging models most often assume that animals should maximize the long-term net rate of energy gain, g , defined as $g = (G - C)/T$ where G = gross energy gain, C = costs involved in foraging, and T = time spent foraging. It seems plausible on a priori grounds that foraging animals should behave according to this goal function, because it results in maximum benefits for animals constrained by time or energy requirements (Schoener 1971; Stephens and Krebs 1986).

Empirical evidence from a wide range of studies with different animals indicates that this foraging "currency" can in fact explain many observations (see reviews in Krebs et al. 1983; Stephens and Krebs 1986). Only in a few cases, however, have predictions from alternative currencies been compared at the same time. In some of these comparisons, the g -currency was found to be inferior to alternative formulations. For example, in breeding starlings, more accurate predictions of the number of mealworms taken at an experimental feeding site were gained by assuming that the parents maximize net rate of family gain (i.e. including the energetic expenditure incurred by nestlings) than by simple maximization of net rate of delivery (Kacelnik 1984). Similarly, Montgomerie et al. (1984) found that flower choice of caged hummingbirds was consistent with predictions from maximization of net energy per volume of nectar reward. In honey bees (Schmid-Hempel et al. 1985) foraging behavior agreed with the predictions from maximization of net energetic efficiency, e , where $e = (G - C)/C$. In ring-billed gulls (*Larus delawarensis* Ord 1815) (Welham and Ydenberg 1988) and male Calliope hummingbirds (*Stellula calliope* Gould 1847) (Tamm 1989), behavior close to efficiency maximization also was observed. This indicates that in certain cases animals may be more sensitive to energetic costs associated with foraging (which is weighed more in predictions from maximization of efficiency) than to time costs (which is more important with maximization of gain rate). Still other currencies, e.g. maximizing daily energy intake, or gross rate of gain, have been analyzed. These currencies reflect differences in the sensitivity of the foraging process to different parameters, e.g. the rate at which parents can feed themselves, or the absolute value of prey items (Houston 1987). Each of these foraging currencies therefore implements different assumptions about the relationship among energy, time, and eventual fitness.

A logically distinct class of models relates to risk sensitive decision making (see Stephens and Krebs 1986). Animals in variable environments have been shown to prefer food sources that are likely to minimize the risk of energetic shortfall (Caraco et al. 1980; Barnard and Brown 1985). Also, workers of social bees and wasps seem to prefer flowers that offer constant rather than variable rewards (Waddington et al. 1981; Real 1981; Cartar and Dill 1990b), and preferences may change with colony conditions (Cartar 1991). Under these conditions, short-term rules that are energy cost-sensitive could be selected for, if variation in energy gain is the primary source of variation in a forager's income. It is not clear, however, how these rules apply to highly social animals where the failure of individual foragers to collect adequate amounts of resources does not necessarily imply individual death or failure to reproduce.

Also, foraging behavior is usually analyzed in isolation from the colony context and life history considerations. But organisms only reproduce once or repeatedly after a period of growth and development. Foraging should therefore be judged by the contribution it makes for eventual reproductive success (Houston 1987; McNamara and Houston 1986), which is not only increased as the animal forages economically but also as it survives until reproduction. Consequently, mortality risks in relation to foraging strategies have to be considered. For example, Werner and Gilliam (1984) and Gilliam and Fraser (1987), using dynamic programming, have suggested that under certain conditions population growth

rates will be maximized by maximizing the ratio R/μ , i.e. the ratio of individual growth rate to predation rate. Habitat choice of fish is consistent with this prediction (Werner et al. 1983). Similar conclusions have been reached by Leonardsson (1991) using static models.

Let us again assume that large colonies have higher fitness, and that maximization of colony population at the end of a cycle requires maximization of instantaneous rate of colony growth, i.e. the difference between birth rate (a function of return rate R) and mortality rate of workers in the colony (Houston et al. 1988). Both quantities, however, are directly influenced by choice of foraging strategy z as illustrated by the return [$R = R(z)$] and mortality [$\mu = \mu(z)$] functions in Figures 2 and 4. To maximize growth rate, foragers should thus choose an instantaneous strategy z^*_1 , which is less than the net rate-maximizing strategy z° , but which maximizes the difference between R and μ (as illustrated in Fig. 4). Foraging-dependent mortality costs could thus explain why animals use strategies with lower immediate payoffs. As a corollary, animals should also vary their foraging efforts in relation not only to mortality costs, but also to expected fitness gain (e.g. variations in the R -curve; see Wolf and Schmid-Hempel 1990).

This prediction of maximizing a quantity related to the difference $R - \mu$ is different from what is predicted by the maximization of the ratio R/μ as suggested by Werner and Gilliam (1984). In fact, the latter seems to fit the analysis of organisms with solitary lifestyle where individual death normally means failure to reproduce in isolation from interactions with close kin. In highly social insects, however, individual death is only loss of energy, time, or work capacity from the colony's perspective, but does not block the propagation of genes through close relatives. Moreover, whereas the ratio R/μ rule lends itself more readily to derive a short-term rule of efficiency maximization, the difference $R - \mu$ rule seems closer to a net rate currency. Hence, it remains to be discussed why an empirically verified strategy, z' , close to maximization of net energetic efficiency, as found in foraging honey bees (Schmid-Hempel et al. 1985), could be identical to a theoretically expected strategy, z^*_1 , maximizing the difference $R - \mu$, the colony growth rate, as derived from life history considerations for social insects. One possibility to resolve this problem would involve detailed measurements of foraging costs, benefits, and mortality rates in the field, and to test empirically whether the various strategies lead to very similar predictions, hence whether situations are common where alternative currencies become indistinguishable empirically. Such detailed knowledge is currently not available for any of the animals so far studied.

The theoretical expectation (i.e. maximizing the difference $R - \mu$) could nevertheless be reconciled with the empirical observation of a cost-sensitive foraging behavior (i.e. maximizing the ratio R/μ) if certain constraints are observed (Drent and Daan 1980). Suppose that birth rate of new workers in the colony is proportional (with constant k_1) to the rate of net energy gain, $E/T = (G - C)/T$ (with $E = G - C$, as defined above), from foraging. Let mortality rate, μ , similarly depend on rate of energetic expenditure associated with foraging, C/T . With this simplification, $R = k_1(E/T)$ and $\mu = k_2(C/T)$ (where $k_2 =$ a constant; Fig. 4). In these terms, the model of Houston et al. (1988) defines an optimal z^*_1 to maximize a function $f_1(z) = k_1(E/T) - k_2(C/T)$. The observed behavior, however, is predicted by a foraging model that defines z^*_2 to maximize the function $f_2(z) = (E/T) / (C/T)$, and a rate-maximizer should choose z° that maximizes $f_3(z) = E/T$. These three conditions for an optimal z will, in general, not coincide. This is easily demonstrated by evaluating $df/dz = 0$ for the three functions, which yields (with notations as above) the condition for z^*_1 to be $dR/dz = d\mu/dz$, for z^*_2 to be $dR/dz = (R/\mu) \cdot d\mu/dz$, and for z° to be $dR/dz = 0$. Provided that $R/\mu > 0$, $dR/dz > 0$, and $d\mu/dz > 0$, as illustrated in Figure 4a, we would therefore predict that $z^*_2 < z^*_1 < z^\circ$.

The situation becomes more interesting, however, if the cost curve is not so smooth as assumed in Figure 4a, but looks more like the step function shown in Figure 4b. Under these conditions a forager that keeps to Houston et al.'s (1988) criterion z^*_1 in a 'sparse'

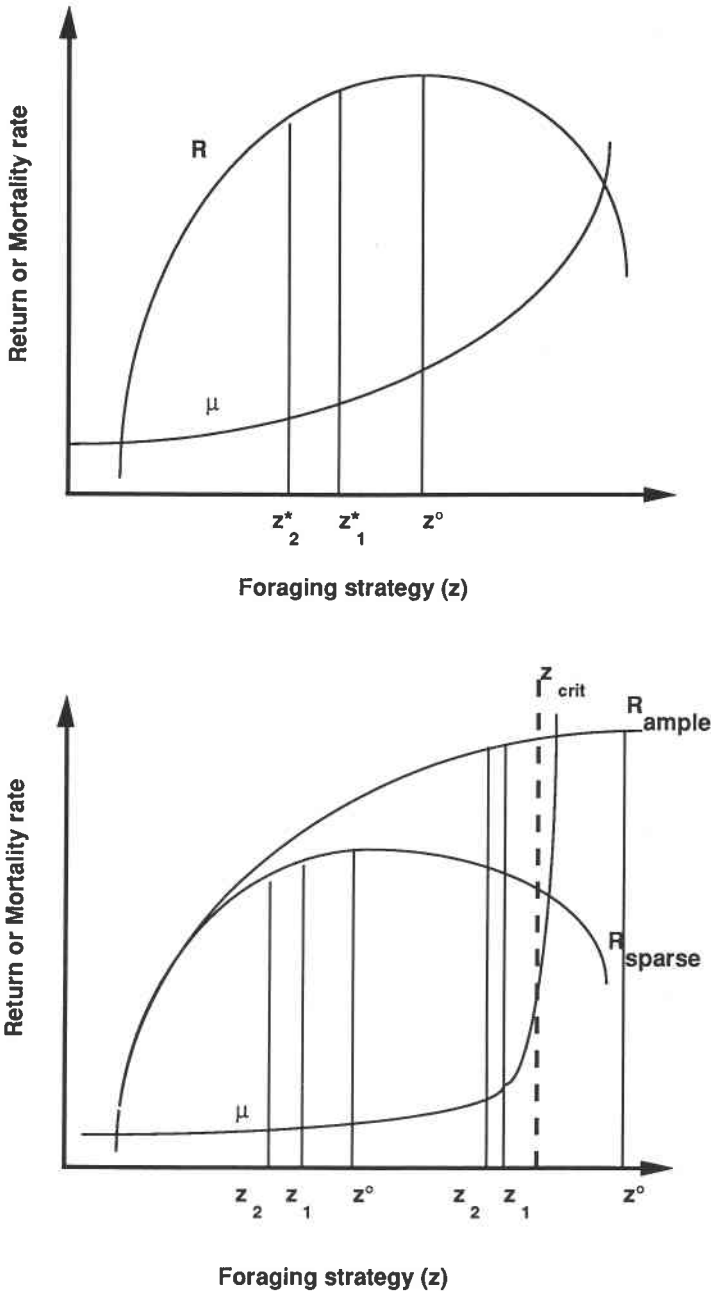


FIG. 4. Return (R) and mortality (μ) rate as a function of foraging strategy (z). Strategy z° maximizes the net rate of resource gain; z^*_1 maximizes the difference $R - \mu$; z^*_2 maximizes the ratio R/μ . The top graph illustrates a smoothly increasing mortality function, whereas in the bottom graph mortality rate is discontinuous, i.e. rapidly increasing beyond z_{crit} . In the latter case, z_{crit} is either high or low relative to the peak in R ("sparse" or "ample" environment). These two situations need to be distinguished for the analysis.

environment as depicted in Figure 1*b* should behave close to the rate-maximizing strategy z^o but not to the efficiency-maximizing strategy z^*_2 , because $d\mu/dz$ is small and R/μ may be large. However, if the environment is "ample" (or the threshold z_{crit} in the cost function low by comparison), working near point z_{crit} will simultaneously maximize the difference criterion (Houston et al. 1988) (i.e. z^*_1) and the (empirically inferred) ratio-maximizing z^*_2 . More formally, near z_{crit} the value of $d\mu/dz$ becomes very large but $dR/dz > 0$, which renders z^*_1 close to z^*_2 , and the point z^o (i.e. $dR/dz = 0$) cannot be reached without $\mu > R$. This particular cost function would thus reconcile predictions from models of short-term foraging behavior which assume maximization of energetic efficiency with predictions generated by models that are based on life history considerations.

Step-like cost functions as depicted in Figure 4*b* may actually be quite common. For example, the energy and time that crabs need to crack mussel shells are fairly constant over a wide range of shell thickness, but rapidly increase thereafter (Elner and Hughes 1978; Juanes and Hartwick 1990). Similarly, the handling time needed to extract a standard amount of nectar is roughly constant, but rapidly increases when corolla depth of the flower exceeds the length of the bumble bee's proboscis (Harder 1983, 1986). In these cases, morphological constraints cause the kind of discontinuous cost function envisaged here. A similar discontinuity relating to body condition has been suggested for parental effort in birds (Drent and Daan 1980) and in the case of the honey bee by Schmid-Hempel and Wolf (1988) and Wolf and Schmid-Hempel (1989). The pattern could result from a constraint on the maximum sustainable work load, which is ultimately limited by the capacity of the physiological "machinery" as hypothesized by Daan et al. (1990; see also Kirkwood 1983).

In the case of the crabs and bumble bees, morphological specialization, i.e. matching the size of claw and mussel, proboscis length and corolla depth, against the background of resource competition is a likely selective force that could shape the cost curves over evolutionary time scales. It is less clear, however, what physiological specialization would lead to discontinuities in survival probability as a function of average daily work load. Moreover, the type of relevant environment ("sparse" or "ample" as in Fig. 4*b*) in relation to physiological constraints (e.g. z_{crit}) sets the stage for short-term strategies. In the case of social insects, recruitment techniques may ensure that foragers most often work in places with good food supply, i.e. that they experience an "ample" situation as in Figure 4*b*. To increase the contribution over the life history time scale, workers may therefore do best by working near a cost threshold in such environments, reflected in a short-term behavior that is cost-sensitive rather than time-sensitive.

Some Final Remarks

A large body of independently derived evidence suggests that the individual behavior of workers, and of foragers in particular, is intimately and predictably linked with the state of the colony (Tables 4, 5). This should come as no surprise. However, most investigations have concentrated on particular and ever-repeated aspects of the problem, such as recruitment response or shifts in task allocation. A limited number of studies, and mostly those in recent years, have asked a more subtle question in addition to task allocation: how do individuals vary their work efforts for a given task in response to variation in colony state?

We have elaborated on the concept of "colony state." This concept, although hypothetical, may prove useful to guide further research. Ultimately, though, it must be filled with real life. Some insight comes from existing studies that aid identification of crucial components that are correlated with colony success, i.e. components of colony survival and reproduction (Tables 1, 2, 3). In fact, if the discussion of colony state is to make sense in biological terms, state variables should relate to such components. So far, colony population in terms of worker numbers stands out as a good predictor of fitness. But such limited insight cannot conceal the fact that the field lacks a conceptual framework that can

handle the many isolated observations. The discussion could (but need not) start with the development of a concept of the preferred colony state that is a dynamically changing variable over the life cycle of a colony. A number of pertinent questions could be asked. For example, is it real or is such a preferred state pure fiction? Is it not a state but rather the image of a regulation process? Furthermore, the trajectories of colonies in a natural population may be so variable that intrinsic colony characteristics overshadow any general pattern and have to be taken into account to define an "individually" different preferred state.

To be useful, developing the concept of colony state in a life history context should generate testable predictions. For example, in the effort-versus-number problem of recruitment, the simple analysis would suggest that, in the sense we have discussed above, work load of individual foragers should increase together with the size of the recruited forager force if mutual interference is weak or absent, but should decrease if mutual interference is strong. Such predictions could be tested in an experiment, e.g. by decoupling size of the forager force from strength of interference using various spatial arrangements of the food supply. Similarly, relating individual foraging strategies and how they can be described in energetic currencies to the unfolding life history of the colony could lead to predictions about the role of physiological constraints, environmental contingencies, and work load of individuals.

There can be little doubt then, that, apart from the development of better concepts, empirical knowledge also is needed, such as how worker numbers, worker sizes, work efforts, etc., relate to colony success. Most importantly, a major gap in our knowledge is the very limited evidence concerning the mechanisms of integration. How do workers assess their colony's state, and how do they decide to take action? Such insight is likely to be generated at the interface of fields like sensory physiology and behavioral ecology. Experimentalists should be encouraged to manipulate colony properties on a large scale (as with Wilson's 1983a experiments on *Atta*) and thus to test how hypothesized state variables relate to success or behavioral actions, or both. Experimental disruption of hypothesized communication pathways or signals could help elucidate the underlying mechanisms.

The biology of social insects shows an astounding diversity. Simple models, as presented here, certainly are inadequate to explain the many details. Nevertheless, the most successful strategy in science has been to start with the simple and move toward more complex issues. In social insects, with their bewildering complexity of worker morphs, lifestyles, breeding systems, or division of labor, it seems that one is often inclined to adopt the reverse path of actions. We hope that by asking simple but important questions a point is made in favor of the first approach. This should not keep us from deeply admiring the diversity generated by biological evolution, but merely help us to strive for better pathways to insight.

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