

Foraging and Defence Strategies

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12.1 Introduction

In many habitats, the first animal that a visitor is likely to notice is an ant forager. Ant foraging trails can stretch for hundreds of metres, like pseudopodia from the central body of the colony, searching for and retrieving food. Attempts to interfere with these foraging trails may prompt a rapid and aggressive response from the ants, with individuals readily sacrificing their life in defence of the harvested resources. Such conspicuous activity is, however, only representative of a small subset of the striking diversity of foraging and defence strategies that have evolved in the ants. The goal of this chapter is to discuss the diversity of individual and collective strategies used by ants to find, retrieve, and defend resources. More specifically, we review how ants decide when and where to forage, what individual and collective strategies are used during foraging, and how ants communicate about food sources. Any foraging strategy is, however, only as effective as the defensive strategies that have evolved to safeguard harvested resources. Consequently, we also explore the defensive strategies used in the acquisition and retrieval of resources from the environment, and in retaining them at the nest. While the study of foraging strategies has a rich history, much is still to be learnt, and defence strategies remain a relatively understudied topic. We therefore identify numerous open questions in the study of foraging and defence strategies, and further discuss general approaches for advancing and integrating research in this area in the future.

12.2 Acquisition of resources

A resource acquisition strategy used by ants has to solve several specific problems. Most obviously, a relatively small number of foragers have to retrieve enough food to feed the entire colony. Frequently, less than 10% of workers participate in foraging (the other workers perform brood care and other in-nest tasks, or are inactive, e.g. Dornhaus *et al.* 2008; Robson and Traniello 2002). Contrary to many solitary insects, ants therefore perform ‘central place foraging’: all food must be brought back to a relatively immobile central place, the nest. A large body of theory covers the specific constraints and optimal strategies in central place foraging (Orians and Pearson 1979; Ydenberg and Schmid-Hempel 1994). There is also a discrepancy between the size of the individual foragers and the size of the colony, the ‘superorganism’ that needs to be supplied with food. In other animals, many physiological and ecological characteristics are tightly linked to body size, such as home range or territory (Adams 2001; Jetz *et al.* 2004), metabolic rate, and lifespan (West *et al.* 1999). In ants, both the body size of individual ants and the mass of their colonies may be important. An ant forager will typically forage much farther from its nest than a terrestrial solitary arthropod of the same size, because ant foragers have to cover a foraging range large enough to yield enough food for a much larger organism, the colony. For example, a leaf-cutting ant may travel several hundred metres to a foraging site (Roces 2002). In relation to body size, this is the equivalent of a human travelling 50–100 km (one way) to collect food.

It comes as no surprise that foraging is one of the most costly activities performed by an ant colony. Costs arise not only in terms of energy used, but also in the time spent and the mortality risks faced by workers as they leave the nest and travel great distances. Interestingly, the energetic costs of foraging, relative to the energy gained by this activity, vary widely among species. In harvester ants, the energetic costs of foraging are negligible compared to the energy collected (which is over 1,000 times more than the cost per trip), but in some nectar foraging ants, the ratio of energy gained to energy expended for the trip is only 3.9 (Fewell *et al.* 1996). Some ants may thus need to tightly optimize their energetic efficiency, whereas for others, minimizing the time- and mortality-costs of foraging may be more relevant (Nonacs and Dill 1990).

Mortality among ants that leave the nest is much higher than mortality of workers inside the nest; foragers may face dangers such as predation, parasitism, adverse weather, and simply losing their way (Hölldobler and Wilson 1990; Nonacs and Dill 1990). This has led to the hypothesis that older workers are allocated to foraging because their loss is less costly to the colony than that of younger individuals, which have many work-hours yet to live (Moron *et al.* 2008; see Section 12.3.1). Facing these difficulties of large foraging distances, high energy and other costs, and high mortality outside the nest, ants have evolved a number of strategies to improve their success at finding and retaining resources (see also reviews in Carroll 1973; Detrain *et al.* 1999; Gordon *et al.* 2008; Hölldobler and Wilson 1990; Roces 2002; Traniello 1989; Tschinkel 2006).

12.3 Individual foraging strategies

An ant leaving the nest to forage has to first search for a suitable food patch. Upon discovery, the forager may then have to overcome the prey item or dissect it into manageable pieces and decide what load size to carry. Foragers have to navigate back to the nest, either in a straight line or by retracing their steps; foragers may also memorize the location of a food patch to be able to return there or recruit to it. In addition, before even leaving the nest, forager ants may have to make decisions about the best

time to forage. Solving all these problems is likely to require a mix of innate, species-specific behavioural rules, and learning abilities to be used by worker ants. We review each of these aspects of foraging in the subsequent paragraphs.

12.3.1 Deciding when to forage

Before specific foraging strategies come into play, workers have to decide when to initiate foraging. This can be studied at the individual level (how do individual workers decide when to forage) and at the level of the colony (how many workers are allocated to the foraging task). The mechanisms of task allocation at the collective level are relevant in the study of division of labour, which is not discussed here (but see Beshers and Fewell 2001; Gordon 1996; Tschinkel 2006 for reviews, and also Chapter 10). The decision to become a forager involves trade-offs between exploration and exploitation, and between flexibility and specialization (see Biesmeijer and de Vries 2001; Blanchard *et al.* 2000; Dechaume-Moncharmont *et al.* 2005; Detrain *et al.* 1999; Jaffé and Deneubourg 1992; Robson and Traniello 2002; Tripet and Nonacs 2004). Age (Hölldobler and Wilson 1990), genetic background (Robinson *et al.* 2005a), 'corpulence' (i.e. fat content, Blanchard *et al.* 2000), body size (Wilson 1980), or dominance status (Powell and Tschinkel 1999) may affect the probability that a worker will start foraging, as will cues and signals from the colony that food is available (Table 12.1) or needed (Burd and Howard 2005). Classic studies often claim that age and body size are the main determinants of task allocation; however, the fact that foragers are, for example, on average older than in-nest workers does not prove that task allocation is based on age *per se*; experience or disease may also play a role (Moron *et al.* 2008; Tripet and Nonacs 2004; Woyciechowski and Kozłowski 1998).

At the individual level, the decision to leave the nest to forage in many ant species is related to environmental conditions, in particular external temperature (Hölldobler and Wilson 1990; Traniello 1989; Tschinkel 2006; Table 12.1). Temperature may influence the expected foraging success, and thus the likelihood that a foraging trip will recoup its costs in a number of ways. As largely

Table 12.1 Collective strategies used in food retrieval by ants. See Hölldobler and Wilson (1990: Table 7–8, p. 280) for a more comprehensive list of genera.

Recruitment strategy	Function	Exemplary genera	References
Solitary foraging: Foragers leave the nest individually and do not appear to interact while searching for or retrieving prey.	Presumably this strategy is used if prey are distributed, unpredictable, and can be carried back by a single forager. This strategy is often seen in predatory ants preying on other arthropods.	<i>Harpegnathos</i> , <i>Pachycondyla</i> , <i>Cataglyphis</i>	Hölldobler and Wilson (1990); Maschwitz and Steghaus-Kovac (1991); Wehner (1987)
Tandem running: a successful forager recruits and leads a single ant back to the food source.	Slow recruitment of individual ants to potentially hard-to-find sites, such as new nest sites. Also used in recruitment to food, although possibly less frequently.	<i>Temnothorax</i> , <i>Pachycondyla</i> (Plate 12)	Hölldobler and Wilson (1990: Table 7–7, p. 273); Möglich and Hölldobler (1974)
Group recruitment: a successful forager recruits a group of several nestmates to the resource	May be an evolutionarily intermediate form of recruitment between tandem running and mass recruitment by pheromone trails; often involves both motor and chemical signals from the recruiting forager.	<i>Camponotus</i>	Hölldobler and Wilson (1990: p. 276)
'Mass recruitment' by pheromone trail: successful foragers leave a pheromone trail back to the nest, which is reinforced in a positive feedback and quickly attracts large numbers of nestmates.	Useful if a food source is rich but short-lived, or if it has to be defended from competitors. Depending on the volatility of the pheromone, a certain minimum number of ants are necessary to maintain the trail.	<i>Solenopsis</i> , <i>Monomorium</i>	Beekman <i>et al.</i> (2001); Evison <i>et al.</i> 2008 Hölldobler and Wilson (1990); Tschinkel (2006)
Stable trunk trails: relatively wide, stable trails lead out from the nest and branch into smaller trails to cover a	Often used for stable resources such as plants (where leaves or extrafloral nectaries are harvested); may also be	<i>Atta</i> , <i>Forelius</i> , <i>Pogonomyrmex</i>	Hölldobler and Wilson (1990)

foraging area. Trunk trails may also be cleared of vegetation.	used where a foraging area is systematically covered by a large colony, or as connections between nests of a polydomous colony.		
Army ant 'raids': these include large numbers of ants moving in a unified foraging front that sweeps a tract of forest. A trail network behind the swarm consolidates into a single column of traffic for returning prey to the nest and allows foragers to return to the raid.	Using this strategy, army ants have the strength in numbers to overpower other social insect colonies, or, in a few species, to 'flush out' a wider variety of arthropod prey from the leaf litter.	<i>Eciton</i> , <i>Dorylus</i> , <i>Neivamyrmex</i>	Couzin and Franks (2003); Franks <i>et al.</i> (1991); Hölldobler and Wilson (1990)
Team transport: two or more ants cooperate in transporting items from the resource back to the nest.	Used for arthropod prey that is too large or cumbersome to be effectively transported by a single forager.	<i>Eciton</i>	Anderson and Franks (2001); Franks (1987); Hölldobler and Wilson (1990: Table 10–2, p. 389f)
'Bucket brigades': foragers only transport items a short distance to a 'cache station', where it is picked up by other ants that transport it to the next station.	This strategy is only likely to be used where large colonies harvest large numbers of items that are unlikely to be 'stolen' from caches; it has been observed particularly in fungus-growing ants harvesting leaves.	<i>Atta</i> , <i>Acromyrmex</i>	Anderson <i>et al.</i> (2002); Röschard and Roces (2003)

poikilothermic organisms, ants have an increased metabolic rate and thus not only a higher rate of energy use, but also higher running speed at higher temperatures (Hurlbert *et al.* 2008; Traniello 1989; Tschinkel 2006). However, especially in very hot and dry environments, too high a temperature may cause desiccation and death (Cerdá 1998; Hölldobler and Wilson 1990). In addition, temperature and weather conditions may change the availability of food items; for example, prey arthropods may be inactive at low or very high temperatures, and plant nectaries may produce low yields in cold or rainy

weather, or may dry up during the middle of the day. Most importantly, temperature-dependent foraging by ants provides some of the best evidence for interspecific competition (although this has been debated, see Dunn *et al.* 2007c and Chapter 5). Species occurring in the same habitat often differ in the temperatures, and thus time of day, during which they forage. Competitively dominant ants typically forage in the morning, and other ant species forage at staggered times over the course of the day (Hölldobler and Wilson 1990; Traniello 1989; but see Dunn 2007 and references therein).

12.3.2 Search behaviour

Once a forager has decided to leave the nest, it can start searching for a food source. Most modelling studies of food-search algorithms assume a correlated random walk (a random walk in which the direction of each step correlates with the previous direction of movement, Harkness and Maroudas 1985) rather than a systematic search strategy (such as searching in an expanding spiral; Figure 12.1). This random walk pattern may be modified to become straighter (smaller turning angles) in response to encounters with other ants or lack of encounters with food sources, leading the forager away from the area, or more tortuous (larger turning angles), keeping the forager in the vicinity (Gordon 2002). The optimal tortuosity of the search path is dependent not only on the probable distribution of food sources (Fourcassié and Traniello 1993), but also on the number of cooperative searchers; if many workers from the same colony are foraging in the same area, foragers should use straighter search paths to minimize overlap. Single foragers, on the other hand, perform optimally if they use a tortuous search path to maximize area coverage around the nest without moving too far away, which would increase the costs of the return journey (A. Schmolke and A. Dornhaus, unpublished data). These results from modelling studies predict that ants from larger colonies may differ from those coming from smaller colonies in their search algorithms, a prediction that has yet to be tested empirically.

12.3.3 Orientation mechanisms

While searching, ant foragers have to use strategies to track their location relative to the nest entrance, in order to be able to return there. The ant *Cataglyphis bicolor* in particular has become a standard model system for studies of orientation and navigation (e.g. Müller and Wehner 2007; Wehner and Menzel 1969; Wittlinger *et al.* 2006). *Cataglyphis* ants use a path integration algorithm to keep track of their homing vector. Path integration means that foragers continuously update their memory of the vector (direction and distance) to the nest by measuring the directions and distances that they walk. In many flying insects, such as bees, distance moved is measured by visual perception of rate of movement (called optic flow, Srinivasan *et al.* 2000). This may play some role in distance measurement by ants, but in the ant *Cataglyphis* it was recently demonstrated that a 'pedometer' is used; distance is estimated from the number of strides made (Wittlinger *et al.* 2006, 2007). Direction can be determined using a variety of compass systems, such as the position of the sun or moon, canopy patterns, prominent landmarks, the direction of wind, or the polarization pattern of the blue sky (Collett and Graham 2004; Hölldobler and Wilson 1990; Müller and Wehner 2007). Wood ants (*Formica rufa*), on the other hand, memorize snapshots of landmarks at multiple positions along a route (Collett and Graham 2004). If the ants arrive at a site that matches their stored view, they can retrieve information on the next landmark, and thus follow their learned

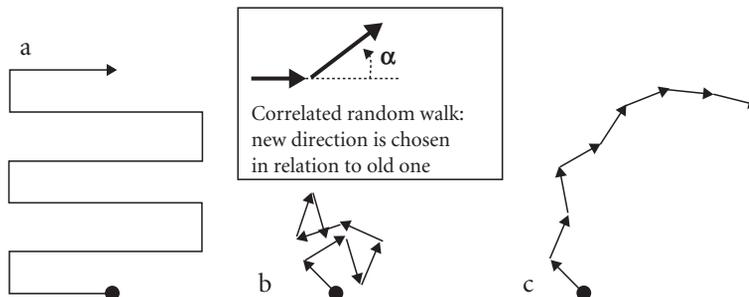


Figure 12.1 Possible search strategies: (a) systematic search, (b) correlated random walk with large turning angles, and (c) correlated random walk with small turning angles. In a regular random walk, the direction of a step is chosen randomly, independently of the direction of previous movement; in a correlated random walk, step directions are chosen from a distribution centred around the previous direction of movement.

route back to the nest from any point along it. Maintaining a library of snapshot landmark memories may be cognitively more costly (in terms of neural tissue or brain capacity required) than a path integration mechanism, but it is also more robust to errors in measurements of distance and direction, and it can be used more flexibly if the ant is displaced from its location by water, wind, or researchers (a condition under which a path integration mechanism fails completely). An even more costly mechanism of orientation may be to use a 'cognitive map', a map-like representation of the relative positions of landmarks, the goal (nest or food source), and the forager's own position (Collett and Graham 2004). It has been debated for a long time whether animals in general, and insects in particular, are capable of using cognitive maps, but new evidence from honeybees suggests that they can (Menzel *et al.* 2006). Such cognitive maps would enable foragers to take novel shortcuts between sites represented on the mental map, something that is impossible if only path integration or route memories are used. Whether ants use cognitive maps for orientation or learn routes based on landmarks, it is clear that learning and memory are important aspects of foraging (Dornhaus and Franks 2008). Learning also enables workers to return to profitable areas at the appropriate time (Schatz *et al.* 1999) or to remember previously found sites for later use or avoidance (Franks *et al.* 2007b).

12.3.4 Load size

Once a food source is located, a forager may have to choose the amount of food that it will bring back to the nest. It may seem that a forager should always carry as much as possible to make the search trip worthwhile, and indeed some species seem to tightly match their loads to forager body size (Powell and Franks 2005), whereas others may use tools to increase their load capacity (pellets of sand functioning as sponges, reviewed in Dornhaus and Franks 2008). However, it has been observed in several social insects that 'partial loads' are sometimes carried back to the nest, in spite of the fact that more food was available at the food source (Roces 2002). This phenomenon has caused some

degree of controversy among researchers. There are several possible adaptive explanations for such partial loads, which either focus on the energetic costs of transport (Ydenberg and Schmid-Hempel 1994; reviewed in Raine *et al.* 2006), on the benefits of recruiting nestmates even at the expense of individual foraging success (Dornhaus *et al.* 2006a; Roces 2002), or on the limitations of the food processing chain at the nest (Burd and Howard 2005).

Many of the predictions of optimal forager behaviour have been derived from modelling studies, particularly in optimal foraging theory (Raine *et al.* 2006; Ydenberg and Schmid-Hempel 1994). In addition to determining the mathematically optimal behaviour, however, it is important to quantify the actual selection pressure or at least the degree to which such optimization can increase foraging success (Raine *et al.* 2006). In many cases, cognitively simpler rules of thumb may work almost equally well. For example, modelling studies predict that foragers may optimally return to the nest with a partial rather than a full load in order to collect information at the nest about possible new, superior food sources (Dornhaus *et al.* 2006a). However, within a parameter range that is biologically plausible for leaf-cutting ants or honeybees, such partial loads would increase foraging success on an average by a mere 0.000002% (ants) or 1–3% (bees) through this mechanism (Dornhaus *et al.* 2006a). It is therefore likely that if partial loads are adaptive, they evolved for another reason than quicker information collection by foragers (e.g. faster recruitment of other foragers or energetic efficiency, Roces 2002). An alternative, non-adaptive explanation is that partial loads simply result from the lack of strong selection for maximizing load size. This may be the case in taxa that do not incur significant energetic costs from foraging (see earlier), or if colony nutrition is limited by factors other than food delivery rates.

12.3.5 Morphological adaptations to foraging

In addition to potentially finely tuned behavioural strategies, ants possess a variety of morphological adaptations for capturing and processing food (see Box 12.1) (Carroll 1973; Hölldobler and Wilson

Box 12.1 Trap-jaw ants

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The success of ants is often attributed to their remarkable social behaviour and cooperation. Group foraging species such as army ants can recruit hundreds or thousands of individuals to defend, divide, and retrieve resources such as a large insect or even a small vertebrate. However, not all ants are social hunters — some of the most successful predatory ants are solitary hunters. How do they compete with the social recruiters for resources? One way is by having some of the fastest jaws in the animal kingdom.

Of the many remarkable cases of extreme feeding ecology in the family Formicidae, few rival that of trap-jaw ants (Figure 12.1.1a). These ants use their oversized jaws and associated catapult-like muscle-firing ability to strike prey with extreme speeds and forces — exceeding 60 m/s and 500 times their own body weight, respectively (Gronenberg *et al.* 1993; Patek *et al.* 2006). These strikes are typically

used for crushing, impaling, de-limbing, trapping, or ejecting prey or competitors. However, some trap-jaw ants in the genus *Odontomachus* can also use their high-powered strikes as an escape mechanism; by triggering their mandibles against the ground, they can launch *themselves* several centimetres into the air in response to threats (Patek *et al.* 2006) (Figure 12.1.1b).

Evolution and Ecology

The term ‘trap-jaw ants’ neither describes a single taxon nor a single clade. In a fascinating example of convergent evolution, trap-jaw morphology has evolved independently at least four times in ants, occurring in at least seven genera from three different subfamilies (Ponerinae, Myrmicinae, and Formicinae) (Figure 12.1.1c). The repeated evolution of this feeding syndrome makes it an ideal system for

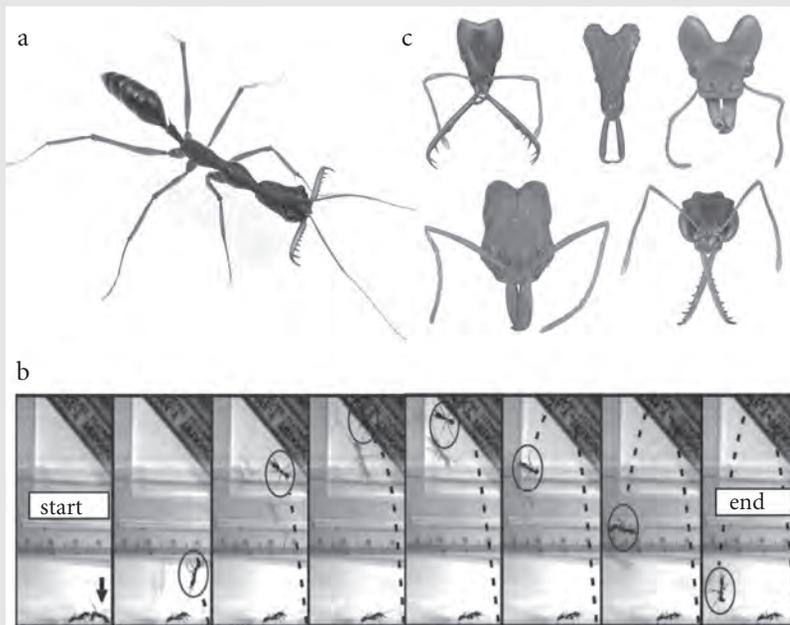


Figure 12.1.1 (a) The trap-jaw ant *Odontomachus coquereli* from Madagascar with its jaws “locked open” and ready to strike. (Photo: Alex Wild). (b) An image sequence of an *Odontomachus bauri* worker “jumping” with her jaws to escape an attacker. (Image: Patek *et al.* (2006) Copyright 2006 National Academy of Sciences, USA). (c) Examples of variation in trap-jaw ant morphology. Top row, left to right: *Acanthognathus*, *Strumigenys*, and *Daceton* (subfamily Myrmicinae); bottom row, left to right: *Odontomachus* (subfamily Ponerinae) and *Myrmoterax* (subfamily Formicinae). (Photos: www.AntWeb.org.)

continues

Box 12.1 continued

understanding the evolutionary prerequisites for, and ecological correlates of, feeding morphology and mechanics. Trap-jaw ants vary in size from a couple of millimetres (e.g. many *Strumigenys*) to over a centimetre (e.g. some *Odontomachus*). They are found in most biomes, but are particularly diverse in tropical and subtropical regions. Trap-jaw ants are commonly found in litter habitats (such as the genera *Anochetus* and *Strumigenys*), but will also nest arboreally (*Daceton* and some *Odontomachus*), and many are ground dwellers living in a variety of habitats including under stones, in rotten logs, and in termite mounds. Trap-jaw ants are highly predatory and most are dietary generalists, preying upon and scavenging a variety of arthropods. However, some species in the genus *Strumigenys* appear to specialize on springtails, while others in the genus *Odontomachus* prey predominately on termites, and a few have even been observed harvesting seeds (Brown and Wilson 1959a; Ehmer and Hölldobler 1995). However, for most trap-jaw ant species, little is known about their natural history.

Morphological and Mechanical Variation

Trap-jaw ants show considerable variation both within and among taxa in terms of mandible size, shape, and the mechanics of storing and generating force (Figure 12.1.1c). The mandibles are elongated and project from the head (anteriorly when relaxed, laterally when cocked), and store energy using a latch or 'click' mechanism. Across trap-jaw species, this

mechanism is built using different anatomical structures, such as modifications of the jaw insertion points in *Odontomachus*, a modified labrum in *Strumigenys* and *Daceton*, which blocks the mandibles from closing, and by interlocking mandibular processes in *Acanthognathus* (Gronenberg 1995; 1996; Gronenberg and Ehmer 1996). In addition to the variation in locking mechanisms, the relative size, orientation, and attachments of mandible opener and closer muscles vary dramatically across trap-jaw ants. Across taxa, the mandible closer muscles can occupy over 60% of the head volume, and are often contained in visible oversized lobes extending the posterior margins of the head. Furthermore, variation in muscle volume is accompanied by variation in the relative composition of muscle fibre types. For example, in some trap-jaw ants, the small trigger muscles that release the strike are among the fastest muscles known in animals (Gronenberg *et al.* 1993). Finally, the shapes and surfaces of the jaws themselves vary considerably among species (Figure 12.1.1c). The jaws may be long or short, narrow or broad. Many trap-jaws are capped by large medially oriented terminal teeth, and the leading edges of the mandibles may also be lined with teeth, which may be sharp or blunt; the leading edges may also lack teeth and have a wedge- or scissor-like surface more suitable for cutting. Whether or not these variations are optimized for capture of certain prey-types, colony defence, or jumping ability is largely unknown and is a rich area for more research.

1990; Powell and Franks 2005, 2006). Aspects of body shape such as relative leg length are likely to be adaptations to the specific mode of foraging employed by the respective species; surface-running ants have longer legs, whereas ants that live in an interstitial environment such as leaf litter have short legs (Kaspari and Weiser 1999; Kronauer *et al.* 2007b; Schönig *et al.* 2005; Weiser and Kaspari 2006). Some species also display worker polymorphism, variation in worker sizes and body shape, producing a worker-caste particularly adapted to a

foraging task (see Plate 10). For example, the leaf-cutting ants in the genus *Atta* produce a range of worker sizes: the largest workers with their strong mandibles cut leaves, other large workers walk fast to transport them, whereas smaller workers tend fungus inside the nest (Wilson 1980). Morphological differences may also occur interspecifically, predicting the diversity and toughness of leaves harvested (Wetterer 1995). Sometimes, very small workers ride on leaves carried by large workers, which may have two important defensive functions

(see Section 12.6.3). Several species also possess ‘soldiers’, that is, workers morphologically specialized for defence (Section 12.6.3).

12.4 Collective strategies in foraging

Ants are eusocial, and collected food is shared among all members of the colony. Therefore, foragers do not operate alone, but are part of a colony-level foraging strategy. There are numerous collective strategies that are used by different species of ants (Table 12.1). These may include recruitment to the food source by pheromone trails and a wide variety of other communication signals.

12.4.1 Recruitment by pheromone trails

Pheromone trails are the most conspicuous, and therefore the best-studied mode of collective foraging in ants. Successful ant foragers in many species lay a trail on their way back to the nest, often by intermittent touching or dragging of the gaster on the substrate. Different ant species use different glands as sources of recruitment pheromone (Hölldobler and Wilson 1990), suggesting possibly many independent origins of this behaviour. Pheromone trails may serve many functions, and not all trails serve to find food and retrieve it; other resources, for example nesting sites (Dornhaus *et al.* 2004), building material (Aleksiev *et al.* 2007), or mutualist plants (Webber *et al.* 2007), are also sought by ants. Furthermore, individual-specific trails may aid in orientation (Hölldobler and Wilson 1990; Maschwitz *et al.* 1986), or be used to measure area of a nest site (Mallon and Franks 2000). Sometimes permanent trunk trails are maintained by ant colonies (Edelstein-Keshet *et al.* 1995), often cleared of vegetation or even reinforced with built structures (Anderson and McShea 2001b). In the most extreme case of the army ants, pheromone trails provide the foundation for an obligate group foraging strategy (Rettenmeyer 1963). Ant traffic on trunk trails can self-organize into separate traffic lanes, which increases running speed (Couzin and Franks 2003); interactions among ants on the trail may also have other functions (Dussutour *et al.* 2007; Gordon *et al.* 2008; see Burd 2006 for a review). In some ant

species, worker ants improve their trail surface or width by plugging ‘potholes’ with their bodies (Powell and Franks 2007) or, more rarely, by forming living bridges (Hölldobler and Wilson 1990). Recent research has shown that in Pharaoh’s ants (*Monomorium pharaonis*), foragers can use the trail branching angles to determine which direction on the trail will lead them back to the nest, and which direction will lead out to the food source (trail polarity; Jackson *et al.* 2004). In the same species, it was also found that ants cannot only recruit using pheromones, but also repel other ants from certain routes, for example to indicate unprofitable areas (Robinson *et al.* 2005a). Subtle differences in the chemical composition of pheromones may in addition indicate who laid them (Jackson *et al.* 2007). The shape of the trail system can be species-specific because of differences in these behaviours, or can be an emergent phenomenon resulting from particular resource distributions (Crist and Haefner 1994; Edelstein-Keshet *et al.* 1995; Franks *et al.* 1991).

12.4.2 Recruitment by tandem running

Pheromone trails, however, are not the only mode of communication available to ants. For example, a well-studied recruitment behaviour that involves both pheromone and mechanical signals is tandem running (Möglich and Hölldobler 1974; Plate 12). During a tandem run, an ant worker leads a single recruit to a resource; the recruit follows the leader closely, frequently touching its antennae to the gaster of the leading ant. If this touching is interrupted, the leading ant will remain in place and wait until the recruit catches up. Because of this feedback between leader and follower, tandem running may fulfil the criteria for ‘teaching’ (Richardson *et al.* 2007). To initiate a tandem run, the scout ant will use both antennation and a ‘tandem calling pheromone’ in the nest (Hölldobler and Wilson 1990; Möglich and Hölldobler 1974).

12.4.3 Other communication

As these examples show, collective foraging has mostly been studied in the context of signals informing recruits about the *location* of food sources or nest sites. However, foragers may communicate

Table 12.2 Categories of morphological defences seen in ant foragers. See also Plate 13 and Hölldobler and Wilson (1990: Table 10–3, p. 393f).

Morphological defence	Function	Associated foraging strategies	Exemplary genera	References
Armour: Thickened exoskeleton, and sometimes associated with a capsule-like gaster (expanded first gasteral segment)	Provides mechanical barriers against crushing, cutting, and puncturing forces exerted by aggressive prey or arthropod enemies	Common in predatory species. Also seen in subordinate omnivores that forage within the territories of aggressive species	<i>Cerapachys</i> , <i>Nomamyrmex</i> , <i>Paraponera</i> , <i>Cataulacus</i> , <i>Procryptocerus</i> , <i>Cephalotes</i> (Plate 13)	Buschinger and Maschwitz (1984); Hölldobler and Wilson (1990); Powell and Clark (2004)
Antennal scrobes: Depressions or cavities on the head that receive the antennae when folded	Provides sheltered protection for the antennae (primary sense organs) when attacking or under attack	Some predatory and slave-making species, as well as subordinate omnivores	<i>Aconthoponera</i> , <i>Harpagoxenus</i> , <i>Cataulacus</i> , <i>Procryptocerus</i>	Hölldobler and Wilson (1990); http://www.AntWeb.org
Shield: Lateral, membranous expansions of the exoskeleton on the head, mesosoma, or gaster	Provides expendable structures that can be seized, chewed, and damaged by arthropod enemies without injury to the ant	Slow-moving omnivores, potentially foraging within the territories of aggressive, territorial species	<i>Cephalotes</i> , <i>Meranoplus</i> (Plate 13)	Andersen (2006); de Andrade and Baroni-Urbani (1999)
Erect teeth and spines: Sharp triangular and elongate exoskeletal projections orientated outwards	May provide mechanical protection against vertebrate predators (spines potentially make the ants painful to capture and eat)	Common in relatively large taxa that forage on vegetation in the understory or canopy in the tropics	<i>Acromyrmex</i> , <i>Atta</i> , <i>Polyrhachis</i> , <i>Cephalotes</i> (<i>atratus</i> clade) (Plate 13)	Buschinger and Maschwitz (1984); de Andrade and Baroni-Urbani (1999) http://www.AntWeb.org
Decumbent teeth and spines: Lobed, triangular and elongate exoskeletal projections orientated along the plane of the body and usually over the main articulation points	May provide protection against arthropod enemies by blocking direct attacks on the main articulation points of the body	Widespread, including taxa that have foraging strategies with high-level interactions with arthropod enemies and low-level interactions with vertebrates	<i>Aconthoponera</i> , <i>Eciton</i> , <i>Phrynoponera</i> , <i>Cephalotes</i> , <i>Meranoplus</i> , <i>Harpagoxenus</i> , <i>Polyrhachis</i> (Plate 13)	Andersen (2006); Buschinger and Maschwitz (1984); de Andrade and Baroni-Urbani (1999); http://www.AntWeb.org
Pubescence: Entire body with a dense covering of long hairs	May provide mechanical barrier to biting attack by arthropod enemies	Appears to be associated with slow-moving, non-predatory species	<i>Apterostigma</i> , <i>Echinopla</i> , <i>Procryptocerus</i> , <i>Meranoplus</i> (Plate 13)	Andersen (2006); http://www.AntWeb.org
Crypsis: Structures that accumulate	Organic debris conceals the ants.	Debris camouflage associated with	<i>Basiceros</i> , <i>Stegomyrmex</i> ,	de Andrade and Baroni-Urbani

(Continued)

Table 12.2 Continued

Morphological defence	Function	Associated foraging strategies	Exemplary genera	References
camouflage material or create a disrupted body outline	Exoskeletal structures, colouration and hairs may disrupt body outlines when ants are motionless	ambush predators. Outline disrupting morphology associated with slow-moving omnivores	<i>Cyphomyrmex</i> , <i>Cephalotes</i>	(1999); Diniz and Brandão (1993); Hölldobler and Wilson (1990); http://www.AntWeb.org

other information, such as *quality* of the resource (McCabe *et al.* 2006; Roces 2002). Communication with nestmates also influences the decision to start foraging: patroller ants may indicate the possible costs (Greene and Gordon 2007a), and successful foraging by others may indicate potential benefits of leaving the nest (e.g. McCabe *et al.* 2006). In addition, several workers may cooperate to transport heavy or unwieldy items to the nest (e.g. Franks 1987; Traniello and Beshers 1991). These 'teams' sometimes comprise workers of different sizes to maximize transport efficiency (Anderson and Franks 2001; Franks 1987; Powell and Franks 2005). Ants may also improve their foraging success by building new nests or moving existing nests into the proximity of stable resources (van Wilgenburg and Elgar 2007).

12.4.4 Ecology and evolution of different foraging strategies

The two factors whose influence on the evolution of foraging strategies has been studied most are spatial resource distribution and colony size. Ants that prey on solitary arthropods, which may be widely distributed across the foraging range and not occur in patches, may have no need for a mass recruitment system (Hölldobler and Wilson 1990). Ants that raid termite colonies, other ant colonies (i.e. predators, like army ants, or social parasites, like slave-making ants), or that exploit other highly profitable, stable resources (e.g. trees in leaf-cutting ants) on the other hand, are likely to benefit from the ability to recruit nestmates in large numbers. In these species, recruitment trails

are common. Pheromone trails can generate a steep increase in the number of ants recruited through positive feedback (if recruits add to the pheromone trail and thus recruit more ants in turn). However, this effect is dependent on a sufficient colony size supplying a large number of potential recruits. In small colonies, pheromone trails may be slow to develop or unstable (Beekman *et al.* 2001; Edelstein-Keshet *et al.* 1995). Colony size may thus predict the complexity of the communication strategy used where pheromone trails are concerned (Beckers *et al.* 1989; Herbers and Choiniere 1996; Maillieux *et al.* 2003), but it is less clear whether colony size has an influence on the benefits of other modes of communication. This is because colony size (i.e. the number of potential recruits at the nest) is irrelevant to the success of a recruitment strategy when the rate of recruitment is not limited by the number of potential recruits. This is the case whenever each forager can only recruit a fixed number of nestmates at a time (Dornhaus *et al.* 2006b), such as in tandem running or small-group recruitment (incidentally, this is also true for the honeybee waggle dance). The evolution of group recruitment and tandem running are thus likely to be determined by factors other than colony size.

12.5 Individual defence strategies

During the act of foraging, individuals use a range of strategies to defend both themselves and any resources they are handling. Individual defence strategies can thus be broadly defined as any morphological, chemical or behavioural characteristic

used against enemies in such a way that it improves the survival and resource acquisition of individual ants. These defences may, in some cases, involve characteristics used in the foraging process, while others appear to depend on adaptations to the special dangers of the taxon's ecology.

12.5.1 Morphological defences

Ant mandibles serve as the primary manipulation-tools in colony life, and they are typically robust and capable of exerting considerable force. The mandibles are therefore of universal importance as defensive weapons, and they are particularly effective in taxa with foraging strategies that have been selected for powerful cutting, crushing, or striking mandible morphologies. Good examples include the scissor-like mandibles of *Atta* leaf-cutting ants, the powerful chewing mandibles of *Camponotus* carpenter ants and the snapping mandibles of predatory genera like *Odontomachus* (Hölldobler and Wilson 1990; see Box 12.1).

In addition to morphological weapons, numerous protective morphological structures have evolved (Table 12.2; Plate 13). While the general function of these structures seems clear, their effectiveness under particular ecological conditions, including against specific types of enemies, have not been explored in detail. For instance, spines, a common morphological defence, are often thought to provide mechanical protection against vertebrate predation (Hunt 1983). Direct support for this hypothesis is lacking, but it seems reasonable for erect spines, particularly as they are common in larger taxa that forage on vegetation (Table 12.2), where predation pressure from birds and mammals is high. Other taxa, however, have lobe-like extensions to the cuticle, teeth, or spines that extend backwards over the main articulation points. These structures may protect against arthropod enemies by providing barriers that block biting attacks on these weak areas. This may be the case in army ants, for instance, where backwards-projecting vertexal lobes or teeth on the head prevent direct strikes by their ant prey (S. Powell, personal observation). Likewise, dense hairs are another common, but poorly understood morphological defence. While hair can be important for



Figure 12.2 Feeding at a rich food resource in *Crematogaster* and *Cephalotes*: *Crematogaster* sp. foragers vigorously defend the food and exude chemical repellents from the tip of their gasters while a heavily armoured *Cephalotes persimilis* forager pushes past the *Crematogaster* sp. defences, apparently without injury. (Photo: Scott Powell)

trapping camouflage material in some ants, other ant taxa have dense covering of long hair that is kept clean (Table 12.2). These may serve as a mechanical barrier against arthropod enemies, in much the same way that plant trichomes provide a mechanical barrier against insect herbivores (e.g. Johnson 1975).

In addition to morphological structures that provide direct defence, warning colouration (aposematism) may serve as a deterrent to some enemies. In taxa like *Pseudomyrmex* and *Myrmecia*, bright and often patterned colouration would appear to be the advertisement of their potent sting (see Section 12.5.2; Hölldobler and Wilson 1990). In other taxa, the bright colouration may warn of distastefulness. For instance, the gynes and soldiers of numerous *Cephalotes* species have brightly coloured gastral eyespots (de Andrade and Baroni-Urbani 1999). *Cephalotes* lack a functional sting, but some evidence suggests that many species produce strongly distasteful chemicals (Coyle 1966; de Andrade and Baroni-Urbani 1999).

12.5.2 Chemical defences

A sting mechanism for venom injection is ancestral (plesiomorphic) in the ants, and remains a

formidable chemical weapon in many extant taxa. The sting is formed by the modification of abdominal segments 8–10, and it is fed defensive chemicals from associated glands, with the venom typically produced in the poison gland (Buschinger and Maschwitz 1984). The sting is a particularly conspicuous weapon in predatory species that use it to kill prey, like many poneroid taxa that hunt solitarily (Buschinger and Maschwitz 1984), and group predators like the ‘New World army ants’ (Ecitoninae; Powell and Clark 2004; Powell and Franks 2005). When threatened, these ants also use the sting as a defensive weapon.

A functional sting has, however, been lost a number of times independently, and the degree to which it has been modified, reduced, or co-opted for other functions is also highly varied (Buschinger and Maschwitz 1984). For example, *Crematogaster* produce venom that does not need to be injected. Instead, it is effective when deposited on an enemy, with the sting little more than an applicator, and it also acts as a repellent (Buschinger and Maschwitz 1984; Marlier *et al.* 2004; Figure 12.2). In other taxa, the sting mechanism and associated glands have been co-opted for non-defensive functions, as in *Atta*, where the poison gland produces only trail pheromones (Buschinger and Maschwitz 1984; Hölldobler and Wilson 1990). In the more extreme case of the subfamily Formicinae, the sting mechanism has been lost entirely and formic acid, still produced in the poison gland, is deposited or sprayed directly onto enemies (Buschinger and Maschwitz 1984). Finally, in the Dolichoderinae, the sting and poison gland are greatly reduced, and a cocktail of defensive chemicals is instead produced in the pygidial gland (also known as Janet’s gland; Buschinger and Maschwitz 1984). Numerous other glands produce defensive chemicals, but these tend to supplement other fighting strategies. Examples include foul-smelling and repellent secretions produced by the paired mandibular glands of many taxa, and sticky metapleural gland secretions in some *Crematogaster* species (Buschinger and Maschwitz 1984). It is interesting to note that taxa with potent chemical defences often lack strong morphological defences, and the most morphologically defended ants

(Table 12.2) tend to have limited chemical weaponry. As Hunt (1983) suggested, morphological and chemical defences may therefore represent alternative evolutionary defence strategies, but this idea has yet to be tested. Similarly, robust analyses of the selective pressures, and particularly the foraging strategies, that favour sting loss have not been conducted. Possible reasons for sting loss include selection for other types of chemical weapons that are more effective against other ants (Buschinger and Maschwitz 1984) and an evolutionary shift in diet away from predation on live arthropods (Kugler 1979). However, exceptions exist for both of these proposed scenarios. Sting loss is therefore likely to result from a number of interacting selective pressures.

12.5.3 Behavioural defences

Behaviour can provide unique defence strategies, and it can also modify and improve the effectiveness of morphological and chemical defences. Bursts of speed are a common behavioural strategy for avoiding danger in the foraging arena, and path complexity or tortuosity may also improve the likelihood of escape (Angilletta *et al.* 2008). These avoidance strategies are likely to be of the greatest importance in taxa where the foraging strategy has selected for high running speeds, such as *Cataglyphis* and *Ocymyrmex* (Hurlbert *et al.* 2008). Diametrically opposite to running is the defence strategy of freezing or ‘playing dead’, and it is typically seen in species with foraging strategies that are associated with slow movement and morphological defences. Examples include *Cephalotes* (de Andrade and Baroni-Urbani 1999), *Meranoplus* (Andersen 2006), and *Cyphomyrmex* (Hölldobler and Wilson 1990). In the case of the arboreal genus *Cephalotes*, body sculpturing and cryptic colouration may help disrupt the outline of the ants, making them even harder to see when they are motionless (Table 12.2; de Andrade and Baroni-Urbani 1999). However, when they visually detect that they have been spotted, or an enemy strikes at them, they use a radically different strategy: they jump (S. Powell, personal observation). Recent work has found that once these falling ants reach a critical speed, they are capable of

Box 12.2 The directed aerial descent of arboreal ants Stephen P. Yanoviak

The evolution of winged flight in insects is unresolved due to a lack of fossil intermediate forms, but was likely preceded by directed aerial descent (i.e. gliding) in an arboreal setting (Dudley *et al.* 2007). Whereas a variety of vertebrates exhibit aerial gliding, the behaviour was unknown in wingless arthropods until it was recently documented in arboreal ants (Yanoviak *et al.* 2005, 2008a). Given that ants are a derived group among insects and are secondarily wingless, their gliding behaviour, while interesting and unexpected, is not directly relevant to the origins of winged flight in insects. However, their abundance in tropical forest canopies, their large variation in body size and morphology, and recent improvements to their phylogenetic resolution make ants an excellent focal group for investigating the selective pressures and aerodynamic mechanisms associated with this remarkable behaviour.

Arboreal ants forage in a relatively exposed physical setting. They may be accidentally dislodged from trees (e.g. Haemig 1997), or may voluntarily drop from branches when provoked (Yanoviak and Dudley 2006; Yanoviak *et al.* 2008a). In preliminary studies in Peru, worker ants composed 66% of wingless arthropods collected in ten passive funnel traps suspended in the forest canopy (Yanoviak, unpublished data). Thus, significant numbers of workers fall as ‘ant rain’ in tropical forests.

Lost workers are costly to ant colonies, and landing in the unfamiliar understory may have grave consequences for arboreal ants. Seasonally flooded forests are common in the tropics and present the most extreme circumstances — fallen insects are immediately consumed by surface-feeding fish. But even dry understory litter may pose a significant hazard. For example, up to 100% of arboreal ants released in the litter were attacked, and up to 40% were killed by the resident litter fauna in preliminary trials conducted in Peruvian terra firme forest (Yanoviak, unpublished data). Thus, the likelihood of a fallen arboreal ant returning to its point of origin after landing in the understory is presumably low, and gliding reduces this loss (Yanoviak *et al.* 2005).

Most research on gliding ants to date has focused on the myrmicine genus *Cephalotes*, especially the common Neotropical species *C. atratus* (Figure 12.2.1). However, at least six other ant genera include gliding species: *Camponotus*, *Cataulacus*, *Daceton*, *Nesomyrmex*, *Procryptocerus*, and *Pseudomyrmex*. Glide performance is generally size-dependent within and among species (Yanoviak *et al.* 2005, 2008a). Specifically, smaller workers within colonies, and smaller species within genera, tend to have larger glide indices (glide index = the horizontal distance travelled per unit vertical drop distance). The consistency of these size-

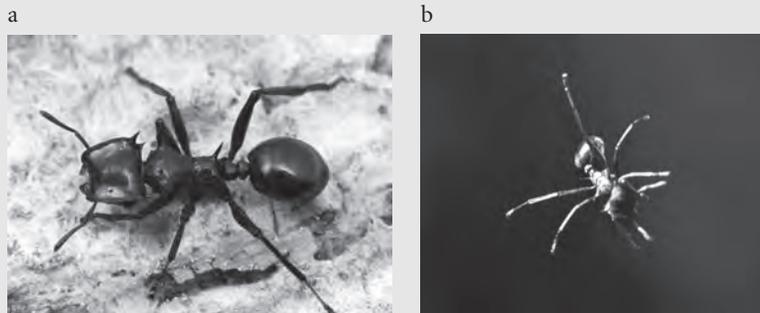


Figure 12.1.2 The Neotropical ant *Cephalotes atratus* (a) is a common inhabitant of rainforest canopies across South America. If a worker of this species is dislodged from the tree trunk it is able to (b) direct its aerial descent back to the tree trunk. (Photos: Alex Wild)

Box 12.2 continued

based patterns largely results from basic physics (i.e. smaller ants reach terminal velocity earlier in a fall). In contrast, mechanisms of aerodynamic stability and glide control are predominately behavioural and differ markedly among taxa. For example, *Camponotus* workers glide toward tree trunks head-first, whereas *Cephalotes* and *Cataulacus* glide abdomen-first (Yanoviak *et al.* 2005, 2008a). The aerodynamic relevance of different appendages during a fall also differs among taxa. Experiments with *C. atratus* suggest that the hind legs are necessary for aerodynamic stability in a fall, whereas field observations indicate that the forelimbs may serve this function in some *Camponotus* (Dudley and Yanoviak, unpubl. data).

Given that not all arboreal ants glide, and not all ants glide in the same manner, what traits can be associated with this behaviour? Gliding taxa share four characteristics: (a) costly workers (relatively small colony size and large per-worker investment); (b) arboreal nesting (ground-nesting arboreal ants like *Atta* and *Paraponera* do not glide); (c) good vision; and (d) diurnal activity (Yanoviak *et al.* 2005). The

latter two characteristics are necessary for targeting during a fall. No nocturnal ants are known to glide, and falling *C. atratus* depend on visual cues to orient to light-coloured objects (e.g. lichen-covered tree trunks; Yanoviak and Dudley 2006). All available evidence indicates that gliding has multiple independent origins in ants. Comparative phylogenetic analyses and more information regarding the ecology, natural history, and morphology of arboreal ants will clarify the selection pressures associated with the behaviour.

In sum, ants provide an excellent model for studying gliding in small, wingless arthropods because they are abundant and experimentally tractable. However, ongoing research shows that gliding is not limited to ants — indeed, directed aerial descent is widespread among arboreal arthropods, some of which may support hypothesized terrestrial origins of insect flight (Dudley *et al.* 2007). Uncovering the mechanisms and constraints associated with the behaviour in ants will facilitate research on less common taxa that are relevant to understanding the evolution of winged flight in insects.

directed descent, returning them to their home tree or nearby vegetation with great reliability (Yanoviak *et al.* 2005; Box 12.2).

12.6 Group defence strategies

While individual defences may improve the survival and resource acquisition of individual ants, they must be put in the broader context of the defensive strategies of the colony as a whole. These group defences, while benefiting from individual defences, can be defined as those that require coordination of more than one individual for success, often at the cost of some of the individuals involved. The coordinated nature of these collective actions achieves defensive effectiveness well beyond the sum of the capabilities of the participating individuals.

12.6.1 Coordinated group defence at the nest

Coordinated group defences are defined here as strategies that use recruitment (pheromonal, tactile, or acoustic) to mobilize a mass defensive response to a specific threat at a specific location. Most ant species display coordinated group defence when an enemy is detected at the nest, but the strength of the response and the degree to which a colony relies on fight or flight depends on the species, life stage of the colony, and the enemy. The universal self-sacrificing behaviour of ant workers is the key in coordinated fight responses because it can increase their overall potency. In many taxa, a fight response is very general, involving widely broadcast alarm recruitment that releases excitement and aggression (Hölldobler and Wilson 1990). However, these responses can be more sophisticated, involving

directed aggression, enemy-specific responses, and cooperative combat strategies. For example, in *Oecophylla longinoda*, multi-component mandibular gland secretions act together to alarm workers, attract them to a point location, and elicit aggressive behaviour (Bradshaw *et al.* 1975). In *Pheidole dentata*, workers recruit nestmates to locations where *Solenopsis* workers have been detected, but show limited or no response to other potential ant enemies (Wilson 1976). Likewise, *Atta* species immediately recruit a massive defensive force when their main invertebrate enemy, the army ant *Nomamyrmex esenbeckii*, is detected, but show no response to other army ants (Powell and Clark 2004). In both *P. dentata* and *Atta*, the defensive response involves a special role for soldiers (see Section 12.6.3), and *Atta* also use cooperative combat strategies to immobilize army ant raiders. In ant–ant fighting, theory suggests that individual fighting prowess and numerical superiority both play key roles in the outcome of a battle, and that their relative importance depends on the type of combat (i.e. a series of one-on-one battles, or an all-against-all war of attrition) that the battlefield allows (Adams and Mesterton-Gibbons 2006; Franks and Partridge 1993). These predictions have been largely supported by observational data from natural large-scale battles (Powell and Clark 2004) and from experimental studies (McGlynn 2000; Plowes and Adams 2005). Further work in this area is likely to prove valuable in understanding the evolution of coordinated group fighting strategies in ants, both at the nest and in the foraging arena.

Flight, or coordinated nest evacuation, is also a common defensive response in ants. Evacuation involves all colony members abandoning the nest with whatever brood they can carry, and seeking temporary shelter until the threat has passed. In some taxa, evacuation is a secondary or simultaneous strategy to fighting; in others, often small colonies or evacuation specialists, it is the first response. In all cases, evacuation appears to be particularly important when ants are under attack by army ants, which may occur frequently for ground-nesting taxa in tropical regions (O'Donnell *et al.* 2007). Thus, while mature *Atta* colonies fight *N. esenbeckii* raiders (Powell and Clark 2004), they resort to evacuation when the army ants enter the

nest, and young colonies immediately evacuate without fighting (S. Powell, unpubl. data). *Aphaenogaster* colonies, on the other hand, tend to take flight as soon as a threat is detected, initiating rapid and highly coordinated evacuation of the entire nest (Hölldobler and Wilson 1990; Smith and Haight 2008).

12.6.2 Coordinated group defence when foraging

In the foraging arena, species with a large workforce of aggressive workers often recruit a strong defensive force to resources that cannot be harvested by individuals. These species are often referred to as 'extirpators' (Hölldobler and Wilson 1990) and the resources that they defend may be depleteable, like large prey items, or renewable resources like honeydew-producing herbivores and nectar-producing plants. Examples include members of the genera *Azteca*, *Camponotus*, *Creमतogaster*, *Pheidole*, *Solenopsis*, and *Wasmannia* (Hölldobler and Wilson 1990; McGlynn 2000), with soldiers playing an important role in resource defence in *Azteca*, *Solenopsis*, and *Pheidole* (see Section 12.6.3). Collective use of chemical weapons can also aid resource defence, both in direct combat with enemies and as repellents around or on a resource (Buschinger and Maschwitz 1984). Interestingly, however, resource defence is mostly directed against other resource-defending species, and is generally ineffective against morphologically well-defended foragers or so-called insinulators. Species of this guild use a combination of stealth and bulldozing tactics to reach and feed at guarded food (Figure 12.2). It is not known how much food insinulators can steal from extirpator species in this way, or whether the lost food has any significant fitness consequences for the extirpators.

In a relatively small number of highly aggressive taxa, a territory is established to provide the colony with exclusive access to resources contained within the territorial border (reviewed in Hölldobler and Wilson 1990; Traniello 1989). Conspecifics, and other potential competitors are excluded from the territory with a number of coordinated border defence strategies. The first is simply the recruitment of a large number of individuals to defend a border

Table 12.3 Ant genera with at least one species that has a morphologically and behaviourally specialized soldier caste. List compiled by cross-referencing Baroni-Urbani (1998), Bolton *et al.* (2006), and Formis 2008 database (Wojcik and Porter 2008).

Ant subfamily	Genera with a soldier caste
Aneuretinae	<i>Aneuretus</i>
Dolichoderinae	<i>Azteca</i> , <i>Philidris</i> , <i>Tapinoma</i>
Dorylinae	<i>Dorylus</i>
Ecitoninae	<i>Cheliomyrmex</i> , <i>Eciton</i> , <i>Labidus</i>
Formicinae	<i>Camponotus</i> , <i>Cataglyphis</i> , <i>Cladomyrma</i> , <i>Gesomyrmex</i> , <i>Melophorus</i> , <i>Myrmecorhynchus</i> , <i>Notostigma</i> , <i>Pseudolasius</i>
Myrmecinae	<i>Acanthomyrmex</i> , <i>Adlerzia</i> , <i>Anisopheidole</i> , <i>Atta</i> , <i>Cephalotes</i> , <i>Carebara</i> , <i>Machomyrma</i> , <i>Monomorium</i> , <i>Orectognathus</i> , <i>Perissomyrmex</i> , <i>Pheidole</i> , <i>Pheidologeton</i> , <i>Solenopsis</i>
Pseudomyrmecinae	<i>Tetraponera</i>

when a threat is detected, as is the case in *Atta* (Whitehouse and Jaffe 1996). In species like *Azteca trigona*, a substantial presence is permanently maintained at the border, with reinforcements recruited when a threat escalates (Albrecht and Gotelli 2001). However, full territorial battles can result in massive mortality on both sides and even colony death (reviewed in Hölldobler and Wilson 1990). In some taxa, this has apparently selected for mechanisms that allow peaceful resolution to territorial disputes. For instance, border marking establishes chemical signals at the territory perimeter that can be honoured by neighbours to prevent unnecessary border skirmishes and escalated aggression (reviewed in Buschinger and Maschwitz 1984; Hölldobler and Wilson 1990). Ritualized combat, on the other hand, allows disputes to be resolved by way of a non-destructive show of force: the colony that displays its numerical superiority wins. Ritualized combat can take many forms, but includes non-escalating fights (e.g. *Cataglyphis niger*, Werner 1976), ritualized fighting behaviours like front-leg boxing (e.g. *Camponotus gigas*, Pfeiffer and Linsenmair 2001) and display tournaments (reviewed in Hölldobler and Wilson 1990).

In discussing coordinated group combat strategies in ants, the special case of repellent and propaganda pheromones that have evolved in arms races between ant predators and their ant prey is worth noting. These chemical weapons, used in a coordinated group context, neutralize the defensive strategies of the victim species by sending them into

misdirected chaos and, in some cases, fighting each other instead of the enemy (Lenoir *et al.* 2001). Examples include slave-making species like *Formica subintegra* and *Harpagoxenus sublaevis* (Lenoir *et al.* 2001), and agro-predators like *Gnamptogenys hartmani* (Dijkstra and Boomsma 2003).

12.6.3 Defence, soldiers, and self-sacrifice

Colony defence appears to be a powerful selective force in the evolution of polymorphism in ants, with numerous independent origins of a soldier caste within the family. A soldier is defined here as a worker phenotype that is morphologically specialized for the role of colony defence. These individuals all display specialized defensive behaviours, but they can differ significantly in the degree to which their full behavioural repertoire is reduced from that of a standard worker. Building on the list compiled by Baroni-Urbani (1998), and adjusting for recent changes in ant taxonomy, good evidence can be found for a soldier caste in 30 genera from 7 subfamilies (Table 12.3). Among these taxa, soldiers can be categorized as specialized for (a) active defence against vertebrates, (b) active defence against arthropods, and (c) passive defence (i.e. entrance-blocking function) against arthropods (Hölldobler and Wilson 1990). The army ant genus *Eciton* provides the clearest examples of soldiers specialized for defence against vertebrates. These soldiers have long mandibles with recurved tips (Figure 12.3a) that easily

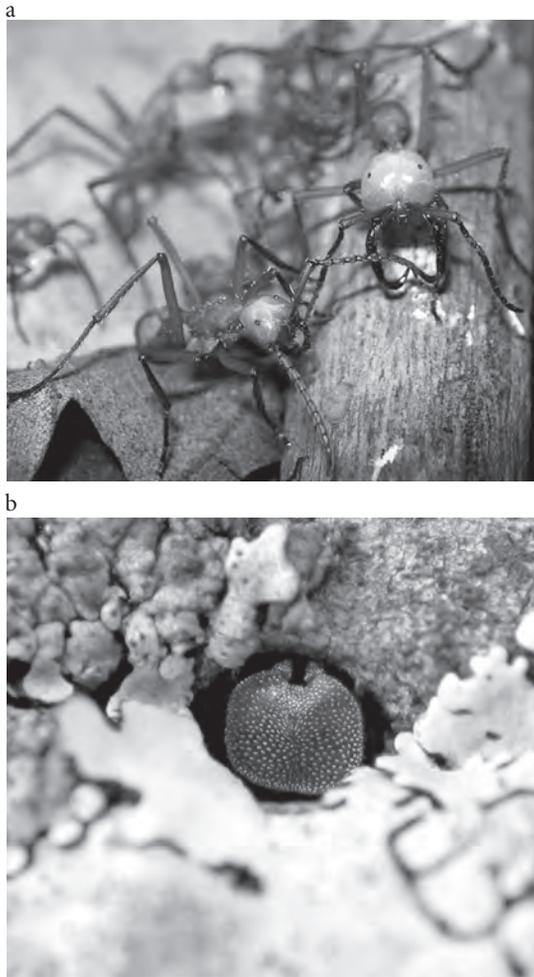


Figure 12.3 Soldiers exhibit a range of defensive behaviours: (a) Guarding of a foraging trail by a soldier in the army ant *Eciton hamatum*. The soldier (right) stands alert as foragers retrieve prey in the background. When a threat is detected, soldiers run in loops at the site of the alarm and immediately bite any vertebrate they encounter. The re-curved tips of the mandibles prevent these soldiers from releasing once they have punctured the flesh of a vertebrate enemy; (b) Entrance blocking by a *Cephalotes persimilis* soldier. These soldiers use their heavily armoured and specialised head-discs to prevent enemies from entering the multiple nests of their colony. Nests are made in pre-existing wood cavities, originally made by wood-boring insects, providing highly defensible structures once soldiers have blocked the entrances. (Photos: Scott Powell)

puncture vertebrate flesh, but the mandible blades lack grasping surfaces for seizing and cutting arthropods (Rettenmeyer 1963). In *Eciton* species that forage diurnally, like *Eciton burchellii* and *Eciton hamatum*, soldiers are deployed at large caches of prey and along foraging trails. In all *Eciton* species that have a soldier, members of this caste travel in a large group around the queen during emigrations, and remain in significant numbers at the nest at all times (Rettenmeyer 1963; Schneirla 1971). Some of the best examples of soldiers that are effective in active defence against arthropod enemies are seen in *Atta* and many *Pheidole* species (Hölldobler and Wilson 1990). A common strategy for soldiers of this type is to dismember their arthropod enemies, which are often other ants, and sometimes this is achieved with the help of smaller colony members (e.g. Detrain and Pasteels 1992; Powell and Clark 2004; Wilson 1976). Finally, the most striking examples of a soldier caste specialized for passive blocking defence at the nest are seen in *Cephalotes*. In the most derived species, the soldier caste has an elaborate disc-like structure on the head that is used to seal the entrances of the pre-existing arboreal cavities inhabited by these ants (Figure 12.3b; de Andrade and Baroni-Urbani 1999; Powell 2008). The basic function of a soldier caste, regardless of type, is clear in most taxa that have one, and one study has clearly demonstrated that the loss of soldiers can dramatically affect colony survivorship (Hasegawa 1993b). However, remarkably little is understood about how the fitness contribution of soldiers differs with environmental conditions and their temporal and spatial availability. Studies that address these types of issues will likely be of great value in understanding why soldiers are a convergent pattern in the evolution of defence strategies in ants.

While soldiers represent the common specialized defensive caste, the so-called hitchhikers provide a unique kind of caste-based defence in *Atta*. Here, members of the smallest caste (often referred to as ‘minims’) ride on leaf fragments being transported by larger individuals, removing fungal contaminants from the harvested leaves (Vieira-Neto *et al.* 2006) and possibly defending transporters against parasitic flies (Feener and Moss 1990; Vieira-Neto

et al. 2006). Adaptations that increase the effectiveness of self-sacrificial defence are also not limited to soldier evolution. The most notable example is seen in the 'exploding' workers of some species in the *Camponotus cylindricus* clade. These ants have greatly hypertrophied mandibular glands that stretch the length of the body. Under conditions of an extreme threat, muscular contractions rupture the glands and the intersegmental membranes so that sticky secretions are released explosively onto an enemy. This defence immobilizes the enemy effectively, but kills the ant (Davidson *et al.* 2007).

12.6.4 Structural defences

In addition to the direct defence strategies employed by ants, constructed barriers or fortification can play an important role in fending off enemies. One of the most basic but common strategies is to seal nest entrances with soil or solid objects like stones or twigs. This is seen in a wide range of taxa, including *Atta*, *Camponotus*, *Cataglyphis*, *Harpagathus*, *Messor*, and *Pogonomyrmex* (Buschinger and Maschwitz 1984; Hölldobler and Wilson 1990; Powell and Clark 2004). Redundancy may also be built into the nesting behaviour of a species by way of polydomy (two or more spatially separated nests used by one colony). Thus, when one nest is attacked, the colony may survive because predators do not locate all nests, or because additional nests provide a secure destination following evacuation of the attacked nest (Debout *et al.* 2007). In species that have the ability to construct their nest in soil or using other material, selection is likely to favour some level of defensive architecture. However, quantitative studies of ant nest architecture are scarce (Tschinkel 2004), and how architectural components may aid defence and increase colony fitness is essentially unknown. A few peculiar defensive nest architectures have been identified, however, with one of the strangest seen in the Neotropical species *Blepharidatta conops*. These ants construct a highly defensible internal chamber that is separated from the other parts of the nest by a wall built from insect carcasses. A single entrance hole is shaped in the defensive wall, and the queen seals the hole with her head, which is morphologically specialized for the task (Brandão *et al.* 2001). Struc-

tural defences can also play a role during foraging. For instance, foragers of *Labidus* army ants bury large food items (Rettenmeyer 1963), and many army ant species build soil tunnels over the stable foraging trail that is used to deliver prey to the nest (Gotwald 1995). In territorial species, so-called barrack nests housing large numbers of soldiers or large workers are built near to the border, with examples seen in *Oecophylla* (reviewed in Hölldobler and Wilson 1990) and *Camponotus gigas* (Pfeiffer and Linsenmair 2001).

12.7 Future directions

In exploring the diversity of foraging and defence strategies in ants, we have identified a number of specific questions that remain unaddressed. However, in considering future work on these topics, we would like to highlight two general directions that we feel are likely to be particularly fruitful. The first is a more explicit integration of ecological context and environmental variation into empirical studies of the efficiency and fitness benefits of foraging and defence strategies. The second is the use of modern comparative analyses to explore the evolutionary relationships between ecology and different strategies.

As discussed, the overall efficiency of foraging strategies in ants can be influenced by numerous components, including when to forage, search behaviour, orientation mechanisms, load selection, and morphology. The evolution of each component in any particular taxon may have been influenced by energy budgets (Fewell *et al.* 1996; Tschinkel 2006; Ydenberg and Schmid-Hempel 1994), mortality risk (Herbers 1981; Nonacs and Dill 1990), competitive environment (see references in Dunn *et al.* 2007c and Chapter 5), spatial and temporal distribution of resources (e.g. Dornhaus *et al.* 2006b; Sundström 1993; see Chapters 7 and 8), and colony size (Anderson and McShea 2001a; Beckers *et al.* 1989; Herbers and Choiniere 1996; Hölldobler and Wilson 1990). However, few, if any, empirical studies have explored how the effectiveness of any particular foraging strategy component varies under a range of realistic ecological conditions that a species might face. For instance, theory suggests that spatial and temporal distributions of resources have

an important impact on foraging strategies (Dornhaus *et al.* 2006b; Raine *et al.* 2006). Yet, we have very little understanding of how ant foraging strategies perform under natural seasonal shifts in resource distributions and availability or across resource gradients within a population. We also have a very limited understanding of if and how foraging strategies undergo adaptive shifts among populations that face distinctly different environmental conditions. Do decisions on when to forage shift adaptively across temperature gradients? Do orientation mechanisms change with habitat structure? Does the relative use of solitary foraging and recruitment change predictably with different resource distributions found at different locations within a species' range? Studies that address these kinds of questions would be ideal for testing theory that explores how foraging strategies should shift with resource distributions. Similarly, the benefits of particular defence strategies relative to particular ranges of environmental conditions, and particularly different kinds of enemies, are very poorly known. Integrated understanding of how the interactions and benefits of foraging and defence strategies change under different conditions is equally rare.

We have also highlighted a number of hypotheses that seek to explain the evolutionary relationships between environmental conditions and particular foraging and defence strategies, and the relationships among strategies. For instance, it has been suggested that dietary shifts may explain the repeated loss of the sting in ants (Kugler 1979), and that morphological and chemical defences may be alternative trajectories in the evolution of defence strategies (Hunt 1983). These ideas, including those new ones suggested by us, are largely based on informal surveys of the diversity of foraging and defence strategies in ants, and have thus not been tested. Modern comparative analyses, which incorporate information about the evolutionary relationships among taxa, provide powerful and robust methods for exploring the relationships among ecological and phenotypic characters, while controlling for the relationships among taxa. The most commonly used methods are those that reconstruct character change over evolutionary time and test for evolutionary correlations among characters.

To date, these methods have not been used extensively to study the evolution of foraging and defence strategies. However, examples include comparative studies of the evolution of recruitment systems in ants (Baroni-Urbani 1993), the evolution of slave-making and the associated propaganda pheromones in the tribe Formicoxenini (Beibl *et al.* 2005; Brandt *et al.* 2006), strata use and its role in the evolution of forager morphology in *Dorylus* (Kronauer *et al.* 2007b; Schöning *et al.* 2005), the role of diet in the evolution of a specialized prey-transport caste in *Eciton* (Powell and Franks 2006), and the role of nesting ecology in the evolution of a specialized soldier caste in *Cephalotes* (Powell 2008). As knowledge of the evolutionary relationships among ant taxa increases (see Chapter 1), the power of these kinds of analyses to test new and old hypotheses on the evolution of foraging and defence strategies will only increase. The patterns identified in these studies also have the potential to inform and focus the kinds of empirical studies of the ecology of foraging and defence strategies that we propose here.

12.8 Summary

Ants and other social insects are model systems for the study of foraging strategies, and have stimulated the development of theories in optimal foraging, central place foraging, risk and robustness, and search algorithms. This is partially due to their abundance and accessibility, and the ease with which colonies can be studied in the field and in the laboratory; but also due to the fascination exerted by their intricate social behaviours. Ant workers may communicate with their nestmates or adversaries using a variety of chemical, mechanical, visual, auditory, or vibration signals, or multimodal signals and cues, which may be specifically directed to single individuals or used to broadcast information and initiate 'mass-recruitment'. This diversity in communication strategies is mirrored by the diversity of food sources used, and in the array of defence strategies that have evolved to improve the acquisition and retention of resources. Many ants are generalists, not only preying on and scavenging a variety of arthropods, but also using nectar or

honeydew sources where available. However, there are also many taxa that have become dietary specialists, feeding on seeds, fungus grown in their own gardens, honeydew produced by tended hemipterans or nectar produced by plants, and even feeding on other ants. Such dif-

ferences in diet, as well as differences in habitat structure, competitive environment, and colony size, have likely led to the broad diversity of foraging and defence strategies in ants. Yet, much is still to be learnt about the process and patterns that underlie this diversity.