

Review article

Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest

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Summary. Insect societies function at various organisational levels. Most research has focused on one or other organisational extreme. At one extreme, it is the adaptive behaviours at the individual level, the behaviour of workers, which is of interest. At the other extreme, colony-level adaptive behaviour and swarm intelligence is the focus. However, between these two extremes, numerous functional adaptive units, or “parts,” exist. These intermediate-level parts include the behavioural properties of “groups” or “teams” in which the functionality only emerges at the group-level and not within the individuals themselves, and also the structural properties of “self-assemblages” in which individuals link themselves together to form an adaptive configuration, such as a living bridge. We review another type of intermediate-level part in insect societies: these are the physical structures that ants build away from the nest. The structures, that are larger than an individual worker but smaller than the colony (hence intermediate), include cleared trails, walled trenches, arcades, tunnels, outstations, shelters, protective pens, shelters over nectaries, food coverings on foraging trails, elevated corridors, and bridges. They are found in a diverse range of species, and are constructed using a variety of materials. We detail the structures built by ants focussing chiefly on the adaptive benefits these structures may confer to the colony.

Key words: Intermediate-level parts, foraging trails, work organization, shelters, tunnels, outstations.

Introduction

Insect societies function at various organisational levels (Anderson and McShea, 2001; McShea, 2001). Most research has focused at the individual level, the behaviour of workers, or, at the other extreme, colony-level adaptive behaviour and “swarm intelligence” (Seeley, 1997; Bonabeau, 1998; Bonabeau et al., 1999). However, functional adaptive

units, or what we here call “parts” (see below), exist at level between these two extremes of the individual and colony, hereafter “intermediate-level.” These intermediate-level parts have received relatively little attention from researchers but will certainly be crucial if we are to fully understand insect society function and organisation.

The concept of a part is perhaps best clarified by example. A “team” (*sensu* Anderson and Franks, 2001) carries out a “team task” meaning that it necessarily requires different individuals to perform different subtasks, i.e. components of the task, concurrently. One such example centres around the tending of the heteropteran *Catenaulella rugosa* by ants. When one of these nymphs is tended by a large ant, such as a *Camponotus brutus* worker, the ant can carry out all the attendant tasks itself: stimulating the nymph’s dorsal glands while collecting the honeydew from the nymph’s anus. For smaller ants, such as *Myrmicaria opaciventris* (Dejean et al., 2000; A. Dejean, pers. comm.), these two subtasks, stimulation and collection, must be performed by at least two individuals working concurrently, one (or more) stimulating the nymph while the other(s) collect(s) the honeydew. In the words of Dejean and colleagues (2000) “one to three workers waited for the honeydew secretion while others moved to the nymph’s side or even climbed onto their bodies in order to palpate the dorsal glands.” This team of workers constitutes a functional unit. The functionality – successful honeydew collection – only appears at the level of the unit itself, the team, but not in the individual components of the unit, the workers (because each individual is too small to do both subtasks concurrently). Also, the members of the team are only a subset of the colony. Hence, this team, (and all teams), is a part.

In contrast “groups” (*sensu* Anderson and Franks, 2001) – another class of intermediate-level parts – involve multiple individuals performing the *same* subtask concurrently. Collective prey retrieval in which the prey items are too heavy for any one individual to transport is a good example of a

group task. The ants complete the task, “transport the prey to the nest,” with multiple individuals pulling on the prey at once. However, unlike teams, groups do not require a discrete division of labour (e.g. Sudd, 1963, 1965).

The set of individuals that tackle a “partitioned task” (reviewed in Ratnieks and Anderson, 1999; see also Anderson and Ratnieks, 2000) is also a part. A task is partitioned when it is split into a number of sequential stages and some material, e.g. a forage item, is passed from one worker to another in a relay fashion. For instance, in the polymorphic weaver ant *Oecophylla longinoda*, small workers collect honeydew from scale insects and regurgitate it to larger workers for transportation back to the nest (Hölldobler, 1984). Thus, honeydew only arrives back at the nest when both sets of workers perform their respective subtasks. Although in this case the individuals could switch among the subtasks, and the tasks could be organised in various other ways (e.g. as parallel-series arrangement, see Oster and Wilson, 1978), the set of individuals form an organisational unit that confers adaptive benefits on the colony.

Groups, teams and members of a partitioned task are parts that confer some behavioural functionality. However, parts may also be physical structures. “Self-assemblages” are adaptive structures formed by individuals linking themselves to one another (reviewed in C. Anderson, G. Theraulaz, and J.-L. Deneubourg, unpubl. ms.). For instance, various ant species do not live in permanent nests but form bivouacs from their bodies within which they shelter the queen, brood and remainder of the colony (e.g. Schneirla, 1971). Numerous other examples of self-assemblages are found in insect societies including rafts, pulling chains, swarms, escape droplets, and defensive doorways. Once again, the functionality only emerges at an intermediate level of organisation and is not present in the individuals themselves; in a sense, each individual is reduced to being but one “building block” of some greater structure which confers the adaptive benefits for the colony (see Anderson and McShea, 2001).

Conventionally, only two hierarchical levels are recognised in insect societies, the individual organism (e.g. an ant) and the colony, with the individual organisms understood to constitute the parts of the colony. Indeed, it is at these two levels that entities are the best defined, or the most highly individuated, presumably as a result of long-continued selection acting at those levels. However, parts may exist at an intermediate level, presumably produced by selection acting on the colony and taking the form of associations of individuals, i.e. subsets of the colony, or structures produced by such associations. An analogous case can be found at a lower hierarchical level: cells are obvious and well-defined parts of multicellular organisms, but selection at the multicellular level has apparently produced intermediate-level parts, i.e. tissues and organs, consisting of associations of cells or of structures produced by such associations. Intermediate-level parts in insect societies can be thought of as the tissues and organs (and related structures) of a colony (Wilson, 1985; Anderson and McShea, 2001).

The aim of this study is to review one further class of intermediate-level parts in insect societies: these are the

physical structures that ants construct away from the nest. These are adaptive structures, “parts,” that are larger than individuals but a subset of the colony and upon which selection does not act directly. We review what structures are built, by which species, using which materials, and where known, under what conditions. In each case, we focus on the likely adaptive benefit that these structures may convey to the colony. We focus on ants because that is where the best data exist and the greatest diversity found. We explicitly exclude nests and other brood-rearing or brood-containing structures such as domatia – although arguably they may all be adaptive intermediate-level parts – because many of their adaptive features will be obvious to readers and have been considered elsewhere (e.g. Starr, 1991; Anderson and McShea, 2001). [The term “domatia” includes natural cavities provided by ant plants as well as cavities in the pith that are excavated by ants (e.g. Ward, 1991); the latter would class “as away from the nest” structures if they do not contain brood, but it seems that in most cases they do.] The structures we review are rarer, will likely be less obvious to the reader, and consequently have received much less attention in the literature. Moreover, if we are to consider seriously an ant colony as a “superorganism” (e.g. Wheeler, 1928; Wilson, 1971; Wilson and Sober, 1989), then these structures – which are built away from the main nest – are crucial in determining the boundaries of such an individual.

Our use of the term part is based on that proposed by McShea and Venit (2001). They define a part as a set of components that are relatively well connected to each other and relatively well isolated from other components. Most objects, including biological objects such as organs in an individual, meet these criteria. Further, some more diffuse entities, what might be called patterns of interaction, are also parts. At the level of the individual, these include physiological cycles and patterns of interaction *among* neurons and muscles, i.e., behaviours. At a higher level, these include patterns of interaction among individuals within a colony, such as team behaviours. Technically, in this definitional scheme, there is no logically necessary relationship between parts and functions; parts may be functional or not (McShea and Venit, 2001). But there are reasons to expect a good empirical correlation between parts and functions (McShea, 2000, in press), and thus here we treat parts as functional units.

Adaptive structures built by ants

Roadways and trenches

When many individuals pass over the same section of soil, well-defined and smooth trails result. In some instances, such trails are an incidental consequence of trail-following behaviour by foraging ants, and as such we do not include these trails as intermediate-level parts. In contrast, many other species construct such trails with seeming intention, actively clearing debris and obstructions. These actively cleared trails increase the speed and efficiency of the workers

as they pass along the trail. For instance, L.K. Johnson and S.P. Hubbell (unpubl. data cited in Rockwood and Hubbell, 1987) found that laden leafcutter ants travel four to ten times faster along cleared trails than across uncleared leaf litter. Examples of such active trail clearing include *Atta* and *Acromyrmex* soldiers that cut up and drag off leaves and twigs that have fallen onto the trail (e.g. Weber, 1972; Gamboa, 1975; Howard, 2001). Howard (2001) suggests that in *Atta colombica*, such large workers (2.2–2.9 mm headwidth) may form a distinct task group within the foraging force. This may also be true of *Pheidologeton diversus* majors (Moffett, 1987); although relatively rare in foraging columns, they appear to play an important role in clearing trails, raising themselves “high on their legs, heaving the object[s] upward with a quick shove of the head.” Other striking examples include *Formica* spp. (e.g. Brian, 1985), *Messor barbarus* (Acosta et al., 1993), and *Pogonomyrmex* spp. (Hölldobler and Wilson, 1990) cutting away living vegetation from the trails.

More active construction behaviour occurs when ants modify trails to become walled trenches. This is known in a variety of ants, most of which appear to exhibit an army ant syndrome (although see Kenne and Dejean, 1999); the walled trenches of *Dorylus (Anomma) wilverthi* (see Schneirla, 1971: Fig. 5.9) and *D. (A.) nigricans* are particularly striking (Figs. 1 a, b). Ants remove pellets of soil from the trail, thus creating the trench, and place them on the perimeter, which creates the walls. Schneirla (1971) reports that in *Labidus praedator*, it is the smaller workers, “trodden upon and rolled underfoot” that do most of the construction by picking up pellets from the trail and pushing them into the growing wall.

Similar behaviour is observed in *Pheidologeton diversus*, a myrmicine swarm-raiding ant that constructs walled trenches 1–3 cm wide (Moffett, 1987). Here too it is smaller workers, the minors and medias, which perform most of the wall construction. Interestingly, Moffett (1987) notes that, ‘most of this material originates from the adjacent trail surface, but workers sometimes deposit material collected at distant points along a trail or out from the sides of the trail. In other cases soil is taken from short, blind-ended tunnels excavated by the ants along the trail. These are “mining operations”, in that the ants appear to use the tunnels solely as a source of building materials.’

In *Myrmecaria opaciventris* these trenches were, on average, 2.5 cm deep after 43 days (Kenne and Dejean, 1999). The adaptive benefit of such time consuming activity is not clear. These walls may drastically reduce the chance of individuals getting lost. They may also reduce desiccation of the ants by providing some shade. Alternatively, these walled trenches may represent an intermediate stage of “arcade” – i.e. a roofed trench – construction (see below). That is, they attempt to build an arcade but only walls persist. Most trench building species either tunnel underground during emigrations, surfacing when conditions are unfavourable for such excavation (Schneirla, 1971; A. Sendova-Franks, pers. comm. w.r.t. *D. (A.) wilverthi*) or construct covered roadways and arcades on the surface. The dampness of the soil appears to affect whether covered arcades or walls are built:

when soil is damp *D. (A.) nigricans* builds arcades, but when the soil is dry, only ragged walls are built (Cohic, 1948 cited in Schneirla, 1971; see also Moffett, 1987). Perhaps this reflects a greater likelihood of roof collapse when the ants attempt to build arcades from dry, and presumably non-adhesive, soil.

Trench construction and trail clearing may represent a large absolute cost to the colony. Howard (2001) estimates 3359 ant hours are required to clear a kilogram of leaf litter from a trail, and Lugo et al. (1973) found that 75% of *Atta colombica* workers on trails are not involved in leaf transportation. They assumed that the ants were involved in trail clearing but further research is clearly needed. However, as such trench construction and trail clearing activity is only observed in species with fairly large colonies, the relative cost to the colony may be very low. The construction costs are divided among the large flow of individuals that use the structure (Howard, 2001), which in the case of *Atta* many persist for many months or even years. In addition, one must also consider the adaptive benefits that these structures may represent, such as improved transportation speed, possible improved trail-laying properties, and the role of the trail itself as a “physical information-storage device” (Shepherd, 1982) that channels workers to profitable sites.

Arcades and above-ground tunnels

Soil arcades, runways, and other above ground tunnels are found in a number of ant species including *Anolepsis custodiens* (Way, 1953), *Atta texana* (Brian, 1983), *Cheliomyrmex* (Wheeler, 1921), *Dorylus* (Schneirla, 1971; Gotwald, 1995; Weissflog et al., 2000), *Formica pratensis* and *F. integra* (Step, 1924), *Labidus coecus* (Rettenmeyer, 1963), *Labidus praedator* (Rettenmeyer, 1963; Schneirla, 1971), *Lasius fuliginosus* (Dobrzańska, 1966), *Lasius niger* (Gößwald, 1985), *Myrmecaria opaciventris* (Kenne and Dejean, 1999), *Nomamyrmex* (Bates, 1905; Rettenmeyer, 1963), *Ochetellus flavipes* (Morton and Christian, 1994), *Pheidole megacephala* (Castiñeiras and Fernandez, 1983), *Pheidole punctata* (Way, 1953), *Pheidologeton diversus* and *P. silemus* (Moffett, 1986a, b, 1987), *P. (laboriosus =) affinis* (G. Rothney cited in Step, 1924), and *Solenopsis invicta* (Clarke and DeBarr, 1996).

Many of the arcade-building species are relatively hypogaeic (subterranean adapted), and as such, are usually photophobic and prone to desiccation. Some may build arcades only when the soil is unsuitable for tunnelling (Schneirla, 1971), but this is not so for all species. More epigaeic (surface-adapted) species, such as the column raider *Nomamyrmex esenbecki*, build arcades when the workers cannot find other suitable cover during their surface raids:

“... it avoids the light, moving always in concealment under leaves and fallen branches. When its columns have to cross a cleared space, the ants construct a temporary covered way with granules of earth, arched over, and holding together mechanically; under this the procession passes in secret, the indefatigable creatures repairing their arcade as fast as breaches are made in it” (Bates, 1905: p. 376).

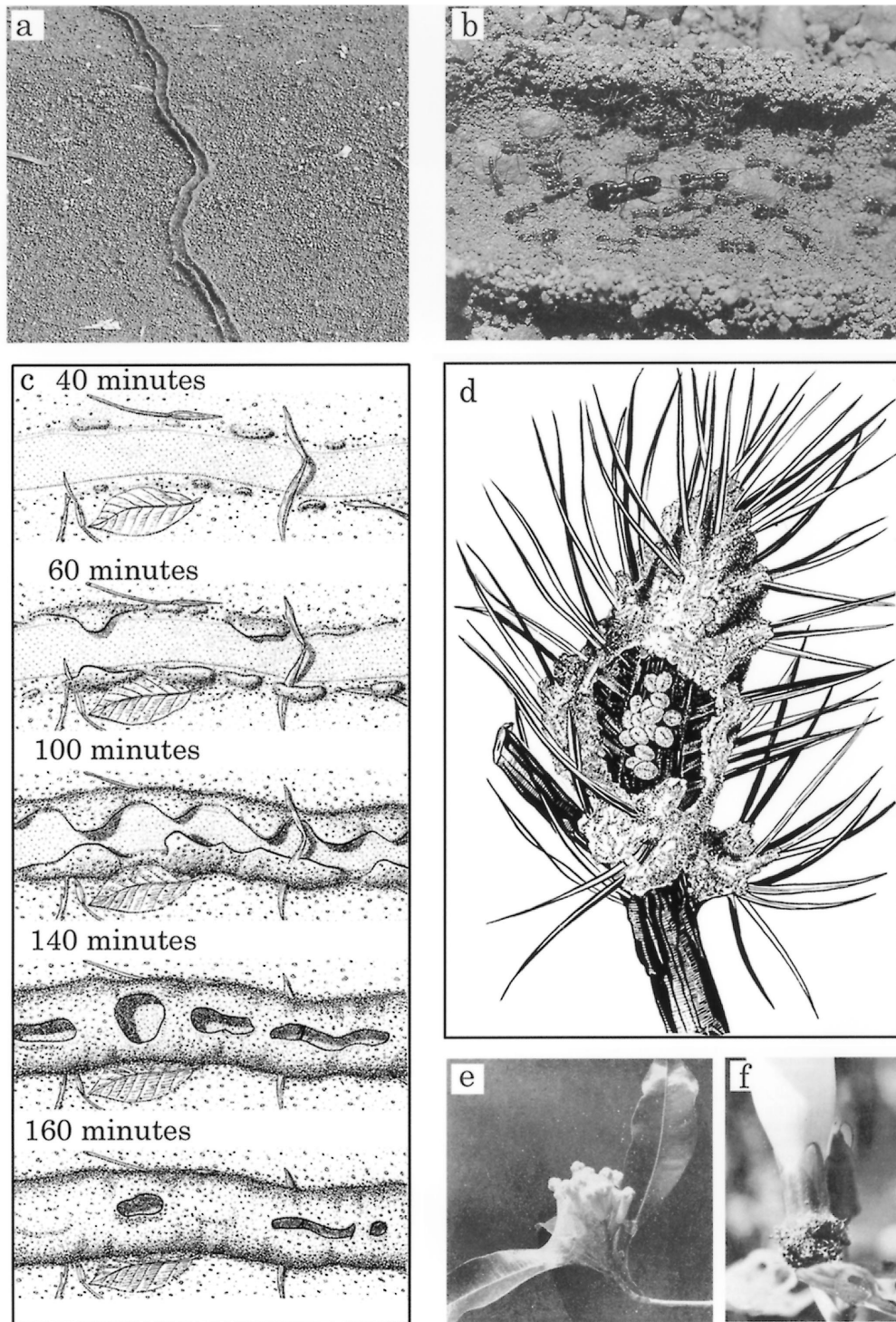


Figure 1. Various structures built by ants away from the nest. a) and b) walled trenches of *Dorylus* (*Anomma*) *nigricans*, courtesy of William H. Gotwald, Jr. c) the time course of arcade reconstruction – minutes after destroying the original arcade by the investigator – in *Pheidologeton diversus* (see Moffett, 1987), courtesy of Theophilus Britt Griswold. d) a carton “cowshed” built by *Crematogaster pilosa* to shelter coccids on a pine shoot, courtesy of Turid Hölldobler-Forsyth. e) a silken shelter built by *Oecophylla longinoda* for the scale insect *Saissetia zanzibarensis* on a clove inflorescence (reproduced with permission from *Bull. Entomol. Res.*). f) a shelter built over the extrafloral nectaries of the herbaceous vine *Ipomoea pandurata* (L.) by *Crematogaster* sp. (reproduced with permission from *Amer. J. Bot.*)

Rettenmeyer (1963) mentions that in the one raid he saw of this species, they constructed about 3 m of covered trail scattered in lengths of 20–40 cm each. He also mentions that *Labidus praedator* and *L. coecus* primarily construct arcades “along the section of trail where the ants left a subterranean route and started an epigeaic one.” In *Pheidole punctata*, earthen runways appear only to be built in the wet season when “it seemed that the exposed [coconut palm] trunk was difficult to climb” (Way, 1953).

Throughout this review, descriptions of construction behaviour are conspicuous by their absence, but arcade and wall construction is one exception. In many cases arcades and walls are constructed without “cement” – such as saliva or faeces, which are used by some termites in their arcades (J. Korb, pers. comm.) – but the soil pellets must be moist to adhere to one another (Moffett, 1987). An important exception is that of Savage (1847, cited in Step, 1924: pp. 149–150) who notes that *Dorylus nigricans* ants “construct arches over their path, of dirt agglutinated by a fluid excreted from their mouth.” *Ochetellus flavipes* constructs runways (and shelters) built of sand bound with resin from spinifex grasses (Morton and Christian, 1994).

Construction of walls and arcades appears to be a stigm-ergic process similar to termite nest construction (e.g. Theraulaz et al., 1999 and references within): first, “the ants [*Pheidologeton*] preferentially deposit soil and debris onto clumps laid down previously” (Moffett, 1987). Second, both sides of the arcade are usually built simultaneously (but see Moffett, 1987), arching over until the walls eventually meet to form the roof (Fig. 1c). In the last step, the ants “contrive, in a surprising manner, to approximate them and fit in the key-stones without letting the loose uncemented structure fall to pieces” (Bates, 1905). Further refinements are noted: *Pheidologeton* medias and majors smooth, or “tamp,” the inner surface with their heads. Moffett (1987) suggests that this activity is primarily directed at low or sagging covers, but such activity may cause some sections of the arcade to collapse. G. Rothney (cited in Step, 1924) notes that majors, who apparently are never involved in building up the walls, play an additional role:

“...I noticed several of the giant workers [*Pheidologeton affinis* majors] ... making their way along the line, and here and there stopping and rearing themselves up against the walls, pressing together and smoothing out in a way which their great size gave them special facility for doing ... I visited this covered way on a good many successive days, and always found the giants busy in this work; they would stand on their hind legs, spread themselves out, and bind together with an even kind of pressure the little blocks of building material.”

Some ants such as *Acanthomyops nigra* (Step, 1924), *Pheidole megacephala* (Castiñeiras and Fernandez, 1983), and *Solenopsis invicta* (Clarke and DeBarr, 1996) (see also Burns, 1964) construct covers over vertical trails which extend from their nest entrances, up the boles of trees or other plants, to their “cowsheds”, shelters for the aphids they tend. These structures are also made of soil but details of their construction are lacking in the literature. They almost certainly involve some binding agent though. Mature *Lasius fuliginosus*

colonies construct above-ground tunnels radiating from the nest running through vegetation such as moss. Dobrzańska (1966) reports that the tunnels (both subterranean and epigeaic) extend for a total of 35 m from the one nest she studied intensively. Many ants species construct tunnels; *Myrmecaria opaciventris* may gradually convert trails to trenches and then to tunnels that may extend 450 m (Kenne and Dejean, 1999). What is of particular interest in *L. fuliginosus* though is that Dobrzańska (1966) reports that older tunnels of more prosperous *L. fuliginosus* colonies are “asphalted” with carton pulp – pieces of wood, dry vegetable matter and soil bound with honeydew (Maschwitz and Hölldobler, 1970). Unfortunately, it is not clear from her description whether this refers to just the walls, the ceiling, or the roadway; either way, this is fascinating behaviour with many possible adaptive benefits. These include improved light-proofing properties, a stronger structure less prone to collapse, and improved ease and speed of travel for the ants.

Outstations

Besides the tunnels constructed by *L. fuliginosus*, they also build “outstations” at the base of trees (Dobrzańska, 1966). These are burrows dug into the soil into which these photophobic ants may rest and avoid sunlight (and bad weather). Some of these burrows are also lined with carton pulp, and perhaps this is another candidate for “wall-papering” in ants (Peeters et al., 1994). Similar outstations have also been observed in *Formica pratensis* and *Lasius niger* (Forel, 1921–1923 cited in Dobrzańska, 1966) and also in *F. integra* (Step, 1924). As a *L. fuliginosus* colony matures and grows, tunnels may be extended to incorporate these outstations with direct links to the main nest (Dobrzańska, 1966).

Interestingly, *L. fuliginosus* exhibits a marked “division of territory” (Dobrzańska, 1966); instead of returning to the main nest after a foraging sortie, workers may spend several days patrolling a foraging area around their outstation. This concentration of workers at various “known” locations means that they may be recruited quickly when needed. Additionally, forage retrieval may often take the form of a partitioned task in which forage is taken to the nearest outstation and transferred to one of its occupants. That new worker then transports the forage to the next station and so on. This relay system allows workers to specialise upon their particular section of territory and move across it “efficiently and faultlessly” (Dobrzańska, 1966).

Hölldobler and Wilson (1977) cite *Oecophylla* as constructing arboreal nest structures that serve as “outposts” within their territories. These authors (1990) also cite the existence of outposts in *Eurhopalothrix heliscata* (Wilson and Brown, 1984) and *Proatta butelli* (Moffett, 1986a) in which groups of workers rest for prolonged periods away from the nest. However, in these two latter cases it is not clear that the ants construct a structure but instead use some pre-existing crevice or other shelter, such as a pile of leaves, opportunistically. Wilson (1971) mentions that in the dacetine ant *Daceton armigerum* “bigger foragers tend to loiter at

way stations between the nest entrance and the hunting grounds, which are located in the forest canopy.” However, no further details (or citation, and there is no mention of such way stations in Wilson, 1962) were given, and therefore one must assume that they do not build shelters until evidence is presented to the contrary.

“Cowsheds”

Since the time of Linné, it has been known that some ants tend aphids (Andrews, 1929). Ants tend a variety of honeydew producing trophobionts, including hemipterans of the ancient sub-order Homoptera (i.e. Sternorrhyncha, Cicadomorpha and Fulgoromorpha) (Wheeler, 1910; Way, 1963; Beattie, 1985; Hölldobler and Wilson, 1990) and heteropterans (Maschwitz and Klinger, 1974; Dejean et al., 2000). Ants also tend lepidopteran larvae – principally of the Lycaenidae (Atsatt, 1981; Hölldobler and Wilson, 1990, but see Maschwitz et al., 1986) – which produce a sweet solution for the ants from their “honey glands.”

Most research in this area has focused on the mutualistic relationships between ants and their trophobionts. What is of key interest in the context of this study however, is that numerous species are known to construct shelters, intermediate-level parts, for their trophobionts (Figs. 1 d, e). These structures are known by a variety of names such as “byres” (Atsatt, 1981), “cattlesheds” (Step 1924), “covers” (Brian, 1985; Clarke et al., 1989), “cowsheds” (Wheeler, 1910; Lobdell, 1930), “galleries” (Seibert, 1992), “houses” (Step, 1924), “nests” (Burns, 1964), “pavilions” (Dorow and Maschwitz, 1990; Dejean et al., 2000), “shelters” (Atsatt, 1981; Clarke and DeBarr, 1996), “stables” (Heim, 1898), and “tents” (Wheeler, 1910). Hereafter we use the term “shelters,” although our personal favourite, “cowsheds” – likely originating from Linné’s nomination of the aphids as *Vaccæ formicarum*, i.e. ant-cows (Heim, 1898) – is certainly a more colourful term.

The shelters, which may house single or multiple individuals (e.g. Burns, 1964 vs. Hölldobler and Wilson, 1990), are constructed from a variety of materials including mud (e.g. Wheeler, 1910: Fig. 206; Step, 1924; McKamey, 1992), sometimes mixed with grass (Burns, 1964), carton (Wheeler, 1910: Fig. 207–209; Dejean et al., 2000), loose bark and wooly covering of pine bark (Mason, 1922), silk (Way, 1954a; Dorow and Maschwitz, 1990), grains of sand bound with resin from spinifex grasses (Morton and Christian, 1994), and twigs (Seibert, 1992). Maschwitz and colleagues (1986) report an unusual example in which *Myrmicaria* sp. ants cover a group of silken shelters, built by its trophobiont *Semutophila saccharopa* (Tortricidae), with a communal earthen roof. Thus, these shelters have a double covering of different materials, one layer constructed by the larva, and another constructed by the ants.

A variety of ant species construct shelters, including *Acanthomyrmex brunnea* (Step, 1924), *A. nigrans* (Step, 1924), *Azteca* spp. (Morrison, 1929; McKamey, 1992; Longino, 1996), *Camponotus brutus* (Dejean et al., 2000; Gibernau and Dejean, 2001), *Crematogaster longispinosa*

(Longino, 1986), *C. pilosa* (Wheeler, 1910), *Formica exsectoides* (Andrews, 1929), *F. obscuripes* (Seibert, 1992), *Iridomyrmex nitidus* (Wheeler, 1910; Atsatt, 1981), *I. humilis* (Lobdell, 1930), *Myrmica ruginodius* (Brian, 1985), *Myrmicaria opaciventris* (Dejean et al., 2000; Gibernau and Dejean, 2001), *Oecophylla longinoda* (Way, 1954a, b, 1963), *Polyrhachis* spp. (Dorow and Maschwitz, 1990), *Pheidole* spp. (Way, 1963), and *Solenopsis invicta* (Clarke et al., 1989). A comprehensive list would certainly be longer; many older references were vague about which species built shelters, particularly in cases where the trophobiont is tended by several ant species. Excavations in the soil at the base of the food plants, such as Andrews’ (1929) “succursals,” in which the arboreal feeding trophobionts may rest are included as shelters. Unfortunately, most references (excepting Andrews, 1929) simply mention that certain ant species build shelters but give little or no detail about the construction behaviour or the shape and size of the structures. This is of interest in its own right because it may provide some insight into why or when such structures are built.

What adaptive benefits might these structures confer to the ants that build them, beyond the basic mutualistic relationship between the ants and trophobionts? The shelters likely protect the trophobionts from predators, competitors, and parasites (Gibernau and Dejean, 2001). This should increase the immediate availability of honeydew to the ants. Shelters may also favour increases in the population size and reproductive rate of the trophobionts (Way, 1963; Beattie, 1985; Dejean et al., 1997) increasing food availability in another way. Because some ants are known to cull their trophobionts when their populations get too large (e.g. Pontin, 1978; Brian, 1983), this could increase the availability of both carbohydrate from the honeydew and protein from the culled trophobionts. Shelters provide protection during foul weather: Beattie (1985: p. 56) states that “several [unspecified] studies have shown that wind, rain or hail may dislodge exposed homopterans, but ants may harvest honeydew from sheltered colonies, even during inclement weather.” Of course, ants themselves also benefit from protection from such weather (Way, 1963), which could dislodge *them* from the plants.

Little information could be found describing when these shelters are built. Clarke and colleagues (1989) mention that *Solenopsis invicta* builds its shelters during autumn, perhaps in response to worsening weather and/or declining trophobiont populations (Way, 1963; Clarke and DeBarr, 1996). Way (1954b) states that *Oecophylla longinoda* builds its shelters in the wet season and concludes that they are probably for the benefit of the ants rather than the homopterans. Whether such shelter construction, which may be costly to the ants, is a risk-averse behaviour is just one of the understudied aspects of these intermediate-level parts.

Protective pens

“Cowsheds” have openings for the ants, and sometimes for their trophobionts, to freely come and go. In contrast, protec-

tive pens are periodically sealed off, sealing in their occupants. Ross (1966) provides a fascinating account of such a shelter constructed for caterpillars of *Anatole rossi* Clench, a butterfly resident of the slopes Volcán Santa Marta in Veracruz, Mexico, by the ant *Camponotus (abdominalis) atriceps* F. The butterfly lays a single egg on its food plant, a small euphorbiaceae *Croton repens*. Upon hatching, the caterpillar spins a silken mat on the underside of a terminal leaf within which it rests during the day and emerges at night to feed upon the leaves. When *C. (abdominalis) atriceps* scouts encounter a caterpillar they recruit nestmates to the plant and within an hour, begin to construct a small depression in the soil at the base of the plant. Once construction is complete, which takes several hours, the ants herd the caterpillar into the chamber, which is approximately 13 mm in diameter and 13–20 mm deep, then seal it, and themselves, inside. Each night at dusk, the ants unseal the chamber and search the plant for other insects, which they remove. Shortly after, the caterpillar crawls up the stem to feed. Just prior to dawn the caterpillar is herded back down into the chamber and sealed in.

Ross's (1966) data suggest that a primary role of the shelter is to protect the caterpillar from predation by the ponerine ant *Ectatomma tuberculatum*. However, interesting additional benefits are also suggested: as winter approaches, the ants resume excavation, deepening the chamber to a tunnel (about 10–15 cm deep) which runs alongside the main tap-root. During this period, the caterpillar remains quiescent, emerging occasionally to feed for short periods. The tunnel presumably protects the caterpillar from the cold. In spring the local Popolucan Indians burn the vegetation to stimulate plant regrowth and prevent succession of the open pine stands (to which *A. rossi* is limited) to climax oak forest. Caterpillars within their ant-constructed chambers generally survive these fires. Indeed, the fires appear to stimulate the onset of pupation. The ants remain with their pupa until a few days before the adult butterfly emerges. During pupation, the ants staff the shelter in shifts (presumably protecting the pupa from predators), each ant remaining in the shelter for no more than 48 h to be replaced by other ants from the main nest. These "pens" thus appear to serve several important roles: they provide significantly better protection from predation than the caterpillar's own silken shelter, and additionally protect it from both the cold of winter and the heat of the fires. Downey (1962) reports similar pens constructed for *Plebus icarioides* (Lycaenidae) caterpillars by the ants *Formica perpilosa* and *F. oreas*.

Extrafloral nectary shelters

Ants also construct shelters over extrafloral nectaries. For example, *Crematogaster* sp. builds shelters from clay and plant-debris on the pedicels of buds of *Ipomoea pandurata* (Beckmann and Stucky, 1981; Fig. 1f). Construction of the shelters begins 2–3 days prior to anthesis (time of flower opening and pollen shedding), and the ants enlarge the shelters as the fruit grows to maintain easy access to the nectaries.

This activity continues until the fruit matures and nectar production ceases. The ants presumably benefit by maintaining exclusive access to the nectaries and supporting plant (Beckmann and Stucky, 1981).

Coverings over food sources on foraging trails

Ants also build shelters over other food sources. For example, *Labidus coecus* is an ecitonine ant that raids primarily through underground tunnels. Rettenmeyer (1963) reports that:

"When *coecus* finds large insect prey which is not readily carried by one or a few ants, it also builds a dirt covering over it. The largest of these were about one centimetre in height and five centimetres across with no supporting pillars."

[See also Weissflog et al. (2000) for possibly similar prey covering behaviour in *Dorylus (Dichthadia) laevigatus*.] He suggests that this behaviour protects the ants from desiccation. Travis (1941) reports similar food-covering behaviour in the fire ant *Solenopsis germinata* in which "plant exudates and other very moist materials are covered with soil particles and plant debris, thus furnishing an earthen canopy under which the ants feed." In *Solenopsis*, a far more epigeic species than *Labidus*, we suggest that the primary benefit may be to limit desiccation of the food rather than of the ants. Rastogi (2000) suggests another benefit of covering food items; he reports that *Oecophylla smaragdina* conceals large prey in trees under piles of leaves and twigs, probably to prevent detection by vertebrate predators. We exclude observations of soil pellets or leaf fragments laid on sticky foods, e.g. Morrill (1972), Fellers and Fellers (1976) and Pierce (1986), because they do not constitute structures.

Elevated corridors and bridges

To cross a gap or stream, ants sometimes link themselves together to form a living bridge, a self-assembly, over which the other members of the colony may pass (e.g. Schips, 1920). However, ants may also construct more persistent bridges from other materials. Jaffe (1983) states "... *Acromyrmex diasi* is adapted to live in swamps where it builds elevated corridors and bridges with grasses to walk and live over the water (Gonçalves, 1982)." W.D. Hamilton once remarked having observed similar behaviour in Amazonian *Acromyrmex* (J.J. Boomsma, pers. comm.). Unfortunately, *A. diasi* is rare and vulnerable to extinction, making further study of this interesting species unfeasible. In this respect, readers are strongly encouraged to report similar construction behaviour (if any) in other swamp-adapted species.

Discussion

We have reviewed a variety of intermediate-level parts, in this particular case, structures that are built away from the nest in ants; these are summarised in Table 1. The structures are diverse: they are found in a variety of species, construct-

Table 1. Summary of the various structures built by ants away from the main nest, and their likely adaptive benefits

Structure	Likely adaptive benefit(s)	Species	References
Cleared roadways	Faster and more efficient movement of workers and transportation of forage	Many, including: <i>Atta</i> , <i>Acromyrmex</i> , <i>Formica</i> , <i>Messor</i> , <i>Pheidologeton</i> , and <i>Pogonomyrmex</i>	e.g. Weber, 1972; Brian, 1985; Moffett, 1986a, b; 1987; Acosta et al., 1993; Howard, 2001
Above-ground trenches, arcades and tunnels	Protection from sunlight, desiccation and weather	Many, including: <i>Acanthomyops</i> , <i>Anolepsis</i> , <i>Atta</i> , <i>Cheliomyrmex</i> , <i>Dorylus</i> , <i>Formica</i> , <i>Labidus</i> , <i>Lasius</i> , <i>Myrmecaria</i> , <i>Nomamyrmex</i> , <i>Ochetellus</i> , <i>Pheidole</i> , <i>Pheidologeton</i> and <i>Solenopsis</i>	For reviews see Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995. For specific references and species see text.
Outstations	Protection from sunlight; quick recruitment of workers; individual spatial specialisation of foraging area	<i>Lasius fuliginosus</i> ; <i>L. niger</i> ; <i>Formica pratensis</i> ; <i>Oecophylla</i>	Dobrzańska, 1966; Forel, 1921/23; Hölldobler and Wilson, 1977
“Cowsheds”	Protection of mutualists and tending workers from inclement weather, parasites and predators	Many, including: <i>Acanthomyrmex</i> , <i>Azteca</i> , <i>Camponotus</i> , <i>Crematogaster</i> , <i>Formica</i> , <i>Iridomyrmex</i> , <i>Myrmica</i> , <i>Myrmecaria</i> , <i>Ochetellus</i> , <i>Oecophylla</i> , <i>Pheidole</i> , <i>Polyrhachis</i> and <i>Solenopsis</i>	For reviews see Wheeler, 1910; Way, 1964; Beattie 1985. For specific references and species see text.
Protective pens	Protection of mutualists from predation and fire/cold	<i>Camponotus (abdominalis) atriceps</i> ; <i>Formica perpilosa</i> ; <i>F. oreas</i>	Downey, 1962; Ross, 1966
Shelters over plant nectaries	Maintain exclusivity of source; prevent phytophagous attack	<i>Crematogaster</i> sp.	Beckmann and Stucky, 1981
Coverings over food items on foraging trails	Limit desiccation of the ants and/or food; maintain exclusivity of source	<i>Labidus coecus</i> ; <i>Solenopsis germinata</i> ; <i>Oecophylla smaragdina</i>	Travis, 1941; Rettenmeyer, 1963; Rastogi, 2000
Bridges	Survival in swampy areas	<i>Acromyrmex diasi</i>	Gonçalves, 1982

ed using many different materials, and may convey numerous adaptive benefits to the colonies that build them. However, can any generalisations be made about conditions that favour their construction? Stability of territories and foraging routes is certainly one factor. It would seem unwise for a *Lasius* colony to “wallpaper” its shelters with carton pulp, or *Messor* or *Atta* workers to cut away vegetation, if a foraging route is only very temporary (Howard, 2001). Similarly, there is little point constructing a shelter if your alate aphids are fickle and likely to fly off to another plant. In all cases the cost of construction has to be weighed against the number of individuals that will use it (e.g. trench), the cost of not constructing it (e.g. cost of predation or desiccation when crossing an open space), or the direct benefit it provides (e.g. exclusivity of nectar access).

Colony size is likely another influential factor. Each individual of a small “simple” (*sensu* Anderson and McShea, 2001) colony may be just too valuable to be spending a significant amount of time away from the main nest; in small colonies, internal division of labour is much more vulnerable to stochastic fluctuations than larger more homeostatic colonies. In addition, construction may be a group task requiring many individuals to work together, e.g. clearing a large twig from a trail, something that is more likely to occur on busy trails from which many individuals may be recruited. Finally, construction may be a team task in which a necessary division of labour is favoured by inherent differences among individuals to complete different subtasks. This is more likely to be expressed in polymorphic colonies, which also tend to be large colonies (Anderson and McShea, 2001). On the other hand, structures built away from a main foraging trail, e.g. a shelter on a plant stem, by just a few individuals may require the workers to be fairly autonomous and individually complex, which conversely tends to be correlated with small colony size (Anderson and McShea, 2001). These issues can only be resolved by gathering additional information about the species that build such intermediate-level parts and the behaviours and algorithms used during construction.

Despite the diversity of structures and diversity of species in which these structures are found, there is a woeful paucity of basic information about this class of intermediate-level parts. We think it speaks volumes that we must resort to the writings of the Reverend Savage, written more than a century and a half ago (1847), for some of the most basic and crucial pieces of information about these structures. As in Tschinkel’s (1991) plea for publication of basic sociometric data, and Ratnieks and Anderson’s (1999) plea for reports of partitioned tasks, we further urge researchers to report examples of, and other information concerning, intermediate-level parts, such as those reviewed in this study.

What is certainly needed is more detail about construction mechanisms. Where such information was available, we observe a good example of convergent evolution: trenches and arcades appear to be similar in both structure and construction behaviour in new world army ants, such as *Labidus*, old world African driver ants, such as *Dorylus*, and Asian marauder ants, *Pheidologeton*. Arcade construction in *Pheidologeton* (a member of the subfamily Myrmicinae) has

certainly arisen independently, but whether this behaviour has independently evolved just once, or multiple times, in the other genera (Dorylines) is not clear (B. Bolton, pers. comm.).

One interesting aspect this review raises relates to Turner’s (1999) concept of the “extended organism”. He argues that organisms can have fuzzy boundaries, that an organism’s sphere of influence may extend beyond its physical embodiment and that it may actively adapt and modify the environment around itself to favour its survival, and that of its genes (Anderson, 2000). He suggests that the nest itself may play an important physiological role, e.g. thermoregulation, and therefore could be considered as an external organ of the colony. Where then, in light of these intermediate-level parts we have reviewed, do we draw the line between nest and non-nest, or colony and non-colony? In the case of an arcade or tunnel that runs from the traditional nest boundary, up a tree and links with an aphid-covering shelter, as in some *Solenopsis*, where is the nest boundary? The same question can be asked regarding the silken tunnels that make up both the nest and foraging area in the ant *Melissotarsus emeryi* (Fisher and Robertson, 1999). Clearly, the structures described above are adaptive modifications of the ant’s environment, and nest/non-nest cannot be as simple as brood containing structures: consider a *Pogonomyrmex* non-brood-containing food storage chamber. Also, *Lasius* workers temporarily living in outstations must be considered as part of the colony even though they are not residing in the nest. Similar logic must surely apply when considering the following: “the colony occupied 263 pavilions at two small bamboo plants” (Dorow and Maschwitz, 1990). Instead of considering a nest of closely connected chambers (or a single chamber in many ant species), should we instead consider it as an “estate” of scattered properties such as shelters? One does not like to muddy the waters unnecessarily, but if we hope to fully understand insect society organisation this issue of nest boundary must be resolved.

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