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Task partitioning in insect societies: bucket brigades

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Summary. There are many ways in which social insect foragers may organise the collection of resources and their transportation back to the nest. One way is to partition the task into a number of sequential stages in which material is passed from one worker to another in a relay fashion. This relatively new concept is known as task partitioning. In this study, we focus on a particular form of task partitioning, bucket brigades, which we define as a multistage (i.e., three or more stages) partitioned transport scheme that uses only direct transfer between individual workers and without any predetermined transfer locations, other than the first or last stages. We first consider the potential costs and benefits of bucket brigades compared to other transportation schemes. We then use theory and computer simulation to analyse some of these aspects in detail. In one empirical study of a bucket brigade, foragers were generally found to be sequenced from smallest (near the food source) to fastest (nearest the nest). This exactly matches what dynamical systems theory would predict as an ergonomically efficient solution. However, we also demonstrate that a single and simple local rule – larger ants win fights over material – will generate this sequencing as an epiphenomenon that is not necessarily optimal. We use the behaviour of bucket brigades to reveal some general points about the optimality of task partitioning in more detail.

Key words: Bucket brigade, task partitioning, forage retrieval, ant foraging, optimal foraging.

Introduction

Insect societies – colonies of ants, bees, wasps, and termites – organise work in a variety of ways. In many situations, an item of work may be an "individual task" (*sensu* Anderson and Franks, 2001) in which a worker toils alone and does not require help to successfully complete her task (Fig. 1a). However, one characteristic that almost certainly has contributed to insect societies' great ecological success (Wilson, 1990) is the ability of individuals to work together. Such cooperative activity takes the form of other task types namely "groups," "teams," and "partitioned tasks" (see Ratnieks and Anderson, 1999a; Anderson and Franks, 2001; Anderson and McShea, 2001a, b; Anderson et al., 2001). In this study, we concentrate on the latter, in particular, focussing on an interesting class of partitioned tasks: bucket brigades.

Task partitioning is a situation in which a task, often forage collection and retrieval (but see Anderson and Ratnieks, 2000 and A.G. Hart, C. Anderson and F.L.W. Ratnieks, unpubl. ms), is split into a number of sequential stages or "subtasks" and material is passed from one worker to another (Jeanne, 1986; reviewed by Ratnieks and Anderson, 1999a). For instance, in the termite *Hodotermes mossambicus*, one set of workers climbs up grass stems, cuts off pieces of grass, and drops them to the ground below (subtask 1) while a second set of workers transports the material back to the nest (subtask 2) (Leuthold et al., 1976). Partitioned tasks are thus characterised by the act of material transfer itself, which explicitly links a number of sequential subtasks. Such transfers may be direct, i.e. the material is handed to the next worker in the sequence, or indirect in which the material is left on the ground, "cached," for others to collect later.

Partitioned tasks vary enormously in insect societies. Task partitioning is taxonomically diverse: examples are known from societies of ants, bees, wasps, and termites (Ratnieks and Anderson, 1999a). Partitioned tasks exist with single and multiple transfer, direct and indirect transfer, and involve a variety of materials (Ratnieks and Anderson, 1999a; Anderson and Ratnieks, 2000). In virtually all cases, however, transfer takes place at some predetermined loca-

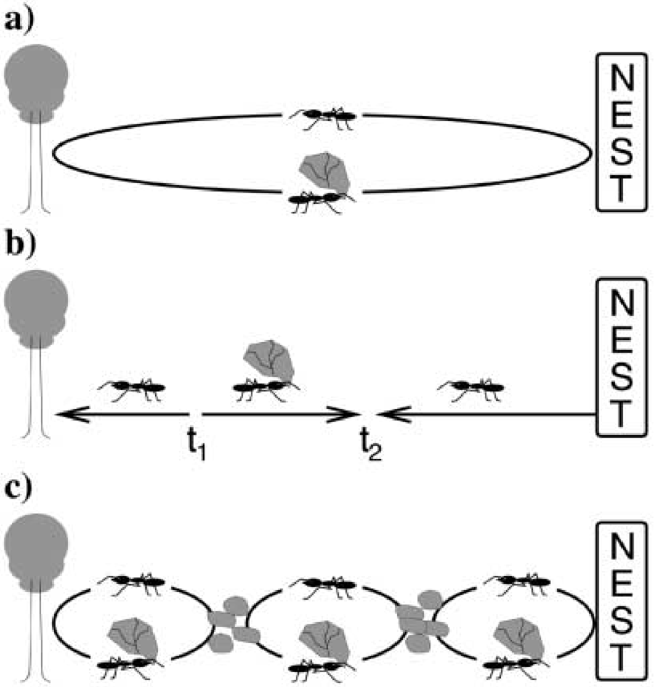

Figure 1. Various forms of forage retrieval. a) Individual foraging, or a parallel-series arrangement. Each individual carries her load all the way from the source to the nest and thus there is no task partitioning. b) A bucket brigade. A worker carries her load along the trail until she meets an unladen ant. Direct transfer takes place (t_1) and the donor ant returns back up the trail while the recipient ant carries the load further down the trail until she meets an unladen ant (transfer t_2), and so on. Transfer is always direct and is not at fixed locations. c) A multistage partitioned task with indirect transfer. Workers transport material, such as leaves, from the source, or a pile of leaves cached on the trail, and drop them at the next cache they encounter on the trail. This is repeated a number of times until the item of forage reaches the nest

tion, such as the forage collection site (as in *Hodotermes* above), at a trail junction, or the nest entrance (Ratnieks and Anderson, 1999a; Hart et al., unpubl. ms). Relatively few examples are known in which transfer occurs in an opportunistic fashion, i.e. where direct transfer takes place at some non-predetermined location (but see Fewell et al., 1992; Ratnieks and Anderson, 1999a).

In this study, we focus on bucket brigades, hereafter BBs, which we consider to be a multistage (i.e., three or more stages) partitioned transport scheme that uses only direct transfer between individual workers and without any predetermined transfer locations, other than the first or last stages (Fig. 1b). This could potentially take place in a variety of situations in colony life including movement of brood, food and other resources between chambers in the nest, and transport of waste materials from the nest. We review the costs and benefits of BBs and use mathematical modelling and computer simulation to consider in greater detail some of the ecological conditions that favour BBs. We also use BBs to make an important but unappreciated point about foraging theory: just because a system matches what is expected under optimal foraging and dynamical systems theory, it does not necessarily mean that it is optimal. It may in fact be an epiphenomenon created by an alternative decision rule that differs fundamentally from the cost-benefit assumptions underlying the optimality model. We use a simple and tractable simulation model to illustrate this. For simplicity, we frame the rest of the study in terms of BBs in forage retrieval in ants, but the arguments and conclusions apply equally well to other potential areas of BBs (e.g., refuse disposal and emigration), and to other social insect taxa.

When we use the term BB with respect to ant foraging, we do not envisage a close-packed line of ants that are able to turn on the spot and pass the item of forage to the next ant in the line (as occurs in human fire-fighting or sand-bagging efforts) although in theory that could be possible. In fact, something very similar does exist in ants: Weissflog et al. (2000: p. 321) describe tunnel excavation in the hypogaeic (subterranean-adapted) army ant *Dorylus* (*Dichthadia*) *laevigatus* in which “soil particles were taken with the mandibles and carried away or pushed backwards beneath the body and passed on to the next worker by backwards movement of the legs.” (This is comparable to tunnelling in some mole-rats [Jarvis and Sale, 1971].) Instead, we visualise a highly dynamic system in which an ant carries her load along the trail until she meets the next unladen ant. As such, there will be no caches or fixed transfer locations, and there will be an undetermined number of transfers. This can result in a system in which continuous adjustments are made to optimise performance (Bartholdi and Eisenstein, 1996). Situations in which transfer is indirect and/or occurs at fixed locations are explicitly excluded because they will always result in some queueing delays. These delays arise when one of the workers is forced to wait for the arrival of a transfer partner and will occur in all but ideal, and hence unrealistic, conditions (Anderson and Ratnieks, 1999b; Ratnieks and Anderson, 1999b). These queueing delays will be absent from BBs because a worker continues to transport material until it meets a suitable transfer partner. (However, workers may still have to queue to obtain material at the source or deposit it at the final destination, see below). In short, workers search for transfer partners while on the move.

Do bucket brigades occur in insect societies?

Bucket brigades, as defined above, do indeed occur in insect societies. Unfortunately, however, we are only aware of a few examples. As we discuss below, we do believe that other examples likely exist and are favoured under certain ecological conditions. BBs may be rare, thus explaining this paucity of information, but we feel that a more likely reason is that task partitioning is a relatively new topic of study and only now are studies explicitly focussing on task partitioning being conducted.

Forage retrieval in the seed-harvesting ant *Messor barbarus* (Reyes and Fernández, 1999; Detrain and Tasse, 2000), in the African stink ant *Pachycondyla tarsata* (López et al., 2000), and in the grass cutting ant *Atta vollenweideri* (Röschard and Roces, 2001, unpubl. data) all meet our criteria for a BB. In all cases, however, such BBs are facultative, i.e., sometimes they occur as a BB *sensu stricto* and at other times as a partitioned task with indirect transfer(s) and/or predetermined transfer locations. Although other *Atta* species have been described as using BBs along foraging trails, transfer is mostly indirect and at set locations and so does not meet our more strict definition (Daguerre, 1945; Fowler and Robinson, 1979; Hubbell et al., 1980; Fig. 1c).

Reyes and Fernández (1999) found that seeds collected by *Messor barbarus* ants were sometimes transferred directly between foragers several times (maximum of 5 transfers) along a 7 m trail. Transfers did not take place at predetermined locations but occurred where an ant encountered another on the trail. (See Detrain and Tasse [2000] for further quantification of such behaviour.) Importantly, material was successively transferred from smaller ants to larger ants. A similar scheme occurs in *Pachycondyla tarsata* but, being monomorphic, the relative size of donor and receiver is not an issue (López et al., 2000). Two factors will contribute to the efficiency of BBs. First, the transferred seed will represent a smaller burden, defined as (seed mass + worker mass)/ worker mass (Rissing, 1982), to the larger ant. Second, larger ants have longer legs, and thus stride length. Reyes and Fernández (1999) found that the seeds were successively transported at a faster rate after each transfer and concluded that this form of organisation "was of great benefit to the colony, in that it considerably reduced the time required for transport to the nest." As will become apparent in later sections, we suggest that such claims should be made with caution.

Footage of subterranean termite foraging, albeit in laboratory setting, is suggestive of BBs (Leuthold, R.H., J. Affolter and B. Hinze: The Biology of *Macrotermes*. Videofilm, University of Berne, Switzerland; see also Affolter, 1999). After collecting material, *Macrotermes subhyalinus* foragers left the foraging site and carried the material back to the nest through a narrow plastic tube. Whenever they encountered another individual coming in the opposite direction there was some interaction between the two individuals, involving at least some antennation. Often this resulted in some sort of "rejection" in which the first forager continued on its way. Sometimes, however, the material would be transferred to the recipient, and the two termites would about turn and return in the direction they had come. As footage exists of a forage item that was twice transferred at non-predetermined locations, simply a section of tubing in which the individuals happened to meet, this qualifies as a BB and thus deserves further investigation.

Advantages and disadvantages of bucket brigades

Advantages

What are the advantages of BBs over other transportation schemes, such as an individual task in which each worker collects material from a source and carries it all the way to the final destination herself (Fig. 1a)? One potentially large benefit is that of enhanced "performance efficiency" (Seeley, 1982; Jeanne, 1986), i.e., the rate at which an individual performs her (sub)task. Task partitioning enhances division of labour (Ratnieks and Anderson, 1999a), and by splitting a task into smaller subtasks, workers are more likely to become specialists and thus more efficient. By definition, a BB will restrict workers to a shorter stretch of the trail (compared to a non-partitioned scenario). Thus, workers may be able to familiarise themselves with the terrain and improve their efficiency in moving over the ground "efficiently and faultlessly" (Dobrzańska, 1966). Each additional partitioning of the task will further reduce the average length of trail that an individual patrols and raise the potential for individual increases in performance efficiency and thus the overall rate of forage retrieval for the whole colony.

BBs also reduce queueing delays at the source and destination. When there is limited access at these places and a series-parallel operation is in place (Oster and Wilson, 1978), queues are bound to occur at some time (Cooper, 1981; Seeley and Tovey, 1994; Hart and Ratnieks, 2000). Queueing individuals are not performing useful work, i.e. collecting forage, transporting it to the nest, or returning to the source. Thus, the group's overall rate of forage transportation to the nest is lower than an equivalent form of organisation in which queues do not occur. However, if there are so many individuals that there is always a queue, even in the long run, then the source becomes limiting and the rate of delivery will be maximised, i.e. someone is always collecting material, the same as in a BB. In a BB, queueing does not occur because just a single individual collects material from the source (i.e. there is no competition for access) and passes it along the line. Similarly, there will be no queueing at the nest entrance, an important consideration given that many nests only have a single entrance for reasons of defence (Hölldobler and Wilson, 1990).

If for some reason workers have difficulty passing each other on the trail then a BB may be advantageous (e.g. Drogoul and Ferber, 1993; Bartholdi and Eisenstein, 1996). For instance, these difficulties may arise because a trail runs through a narrow channel or tunnel in the nest, through carton tunnels that run from the nest to the foraging areas (e.g. *Lasius fuliginosus* ants, Dobrzańska, 1966), or a trail runs along a narrow branch in the canopy. A BB is a system in which a worker carries her item of forage until she meets the next empty-handed forager downstream (on the nest-side of the forage) and transfer occurs. The now empty-handed upstream-worker will then turn about and travel farther upstream towards the forage source. Consequently, workers have no need to pass each other and these "passing delays" are removed. However, this is true only if individuals are sequenced from slowest (nearest the source) to fastest (nearest the nest) – a situation which can easily arise (see below) – because a fast moving worker may become blocked by a slower-moving worker in front of her. In addition to those described above, examples are known in ants in which transfer is direct, seemingly occurs at non-predetermined locations, and after transfer, the donor turns about and continues back towards the food source (*Paraponera clavata*, Fewell et al., 1992; *Acromyrmex octospinosus*, pers. obs.; see also Hart et al., unpubl. ms). However, in these cases it is not known whether further transfers occur, i.e. that this is a multistage process, and thus whether they truly qualify as BBs.

Compared to partitioning schemes with indirect transfer – in which piles of material may accrue (e.g., Hart and Ratnieks, 2000) – BBs minimise the amount of work-in-progress, i.e. the amount of material on the trail at any one time. This may be an important factor if robbing of the material occurs or if material is prone to other losses. Also, because workers do not have to wait at a fixed location they may be less prone to potential parasites, such as phorid flies (e.g. Bragança et al., 1998; Tonhasca et al., 2001; Hart et al., unpubl. ms). In short, uniquely for a partitioned task, in a BB neither material nor workers are delayed and so consequently are always on the move. Moreover, if workers are sequenced from slowest (nearest the source) to fastest (nearest the nest), material *accelerates* as it nears the nest. (However, this effect could be small for items which represent a low burden [sensu Rissing, 1982] to the carriers.) That is, the material is carried by larger individuals who may be better able to protect it and who are presumably faster. In other words, items are less at risk the more effort has been invested in them.

Disadvantages

If BBs have advantages then they also have some disadvantages. One problem in a BB is that the majority of workers will have no influence on the choice of forage items. It is the single worker at the first stage that determines what is transported. In a species with polymorphic workers, such as *Atta cephalotes* and *Messor barbarus*, the ants involved in the forage choice would be unable to optimise the choice to maximise transportation rate: they would not know the distribution of abilities of the other workers in the line. Any item that the first individual chooses is likely to be too small for some of the larger workers – the burden is suboptimal; the ant could work harder – and too large for some of the smaller workers – the burden is supraoptimal; they are overworked and slow. (Obviously, this will be less of a problem in a monomorphic species.) This is not so in a parallel-series scheme in which individual worker chooses an item to suit her abilities (e.g. Baroni-Urbani and Nielsen, 1990; Roces, 1990; Burd, 1996).

Handing off material to another individual in the line introduces delays: the "joint handling times" in Reyes and Fernández's (1999) study. Even though there are no search delays that occur in other task partitioning schemes with direct transfer (Anderson and Ratnieks, 1999a; Ratnieks and Anderson, 1999a), each stage of the BB will involve some delay for the forage as it is transferred between workers. In a BB of n individuals there will be $n-1$ transfers. If each transfer takes an average of h seconds, then a BB introduces a total delay of $(n-1)h$ seconds over and above that experienced by individuals working alone. It is thus clear that an increase in the number of ants and/or the handling delays can potentially greatly decrease the efficiency of BBs compared to non-partitioning unless compensated for by other improvements, such as enhanced performance efficiency (see below).

The advantage, discussed above, of increased familiarity with the terrain in highly subdivided BBs may turn into a disadvantage when there is frequent disturbance of the foraging trail by predators, parasites, or competing social insects. Moreover, an increase in disturbance will tend to generate a higher efficiency cost to specialists than generalists. This is because the more "specialised" a BB becomes (because its members become attached to trail parts that they know better), the more "vulnerable" (in terms of time wasted when restoring a disturbance) the BB will be when the environment becomes partly unpredictable. Thus, at some point such disturbances might start to make BBs less efficient than individual foraging or partitioned foraging with indirect transfer.

Formal analyses

How much performance efficiency is needed to offset handling delays?

As discussed above, handling delays will reduce the throughput of material compared to individual foraging unless offset by other benefits such as performance efficiency. How much performance efficiency though, in terms of transportation speed – that is, their running speed when taking into account all the stops, turns, and other delays – would be required for a BB to be more efficient than a non-partitioned transportation scheme? Suppose that the distance from source to nest is d cm and that under individual foraging retrieval, an ant's average running speed is r cm/s and that in a BB it is R cm/s. (Laden and unladen running speeds do of course differ but as the total amount of distance laden and unladen is the same for both schemes we can just consider the average speeds.) The average time required for the material to reach the nest under the individual scheme is $2d/r$ whereas it is $2d/R + (n-1)\,h$ for BBs. Thus, BBs are faster than individual forage retrieval if $R/r > (2d/r)\,/\,(2d/r - (n-1)\,h)$. The critical relative running speeds, R/r, thus depends non-linearly upon h and n. In other words, each additional ant would require a greater and greater increase in running speed for a BB scheme to be faster. Also, as trail length increases, the critical R/r value decreases, towards the limit of 1, such that any performance efficiency increases have longer to operate, thus favouring BBs. This matches findings by Röschard and Roces (2001) who state that the occurrence of four or more stages in *Atta vollenweideri* was less frequent when trails were short.

Could bucket brigade-like behaviour be an artifact?

Reyes and Fernández's (1999) study demonstrated that *M. barbarus* are generally sequenced from slowest (nearest the food source) to fastest (nearest the nest), as would be predicted as an optimal bucket-brigade arrangement from dynamical systems theory (Bartholdi and Eisenstein, 1996; Bartholdi et al., 1999). However, the "joint handling times," which averaged 11 seconds (range: 4–30 s) each, and recall that there were up to 5 transfers, do not seem indicative of an efficient process. Reyes and Fernández (1999: p. 123) suggest that "During transfer, the transporting worker offers a degree of 'resistance' to giving up the load. This may be a mechanism to ensure that the load is transferred to a larger worker."

In this section we use theory and computer simulation to demonstrate that a very simple individual rule, motivated by the above observations of *M. barbarus*, will generate this sequencing from slowest to fastest as an *artifact* of a self-organised process (Camazine et al., 2001) and not because it makes cooperation more efficient. Thus, we suggest that one should exercise caution when analysing the possible adaptiveness of seemingly optimal transportation schemes, even when the arrangement seems to match theoretical predictions.

The logic of the artifact scenario

Under the following two assumptions: 1) larger ants are faster than slower ants (e.g. Franks, 1985); and 2) an ant can take a food item from a smaller ant but not from a larger one (e.g. Wilson, 1962 w.r.t. *Daceton armigerum*; Rudolph and Loudon, 1986 and Wetterer, 1990 w.r.t. *A. cephalotes*), we argue that the following rule is sufficient to account for the sequencing of individuals from smallest (nearest to the source) to largest (nearest the nest). Size-sorted BBs spontaneously arise if each forager follows this simple myopic rule: *if you are without a food item, run out along the foraging trail until you encounter one and then take it if you can, even if you must wrest it from another ant, and carry it back towards the nest*.

Consider the experience of a large forager. As it leaves the nest, it is likely that the first returning forager it encounters is smaller, and so the larger ant will successfully wrest the food item away and return to the nest. It is unlikely to meet a still larger ant on the way back. Subsequent trips are likely to repeat this experience. On the other hand, a smaller ant is likely to have to travel for a long time before it encounters an even smaller forager that is returning with a food item; in fact, it may have to travel all the way out to the food source to get a food item. As the small ant returns with a food item, it is likely that any forager it encounters will be larger and will take the food item, after which the small ant will return to the food source. Again, subsequent trips are likely to repeat this experience.

A more careful argument goes as follows. Assume that a fixed set of n foragers are engaged in retrieval of food from a single source at unit distance from the nest. Consider the largest forager, which we assume to travel laden at velocity v_n (where $v_n > v_{n-1} > \ldots > v_1$) and unladen at velocity w_n (where $w_n > w_{n-1} > \ldots > w_1$): within time $(1/v_n) + (1/w_n)$ she will carry food back to the nest and from then on, no smaller ant with a food item will ever come between her and the nest. Similarly, within time $(1/v_{n-1}) + (1/w_{n-1})$ the second largest ant will eventually meet the largest ant and from then on, no smaller ant with a food item will ever come between them. Continuing in this way we see that within time $\sum_{i=1}^{n}[(1/v_i) + (1/w_i)]$ the ants must be sorted from smallest (near the food source) to largest (near the nest). Even if unladen velocties do not differ among individuals (for example, as in Rissing, 1982 for *Veromessor pergandei*; C. Detrain, unpubl. data for *M. barbarus*), i.e. $w_n = w$ for all n to give sequencing within $\sum_{i=1}^{n} [(1/v_i) + (1/w)] = {}^{n}\!/_{w} + \sum_{i=1}^{n} (1/v_i)$, the result still stands.

Offering resistance may be a way of ensuring that material is passed only to larger, and therefore faster, ants. It is perhaps not surprising then that Reyes and Fernández (1999) found a significant negative correlation between the joint handling times and the size difference of the two ants: the more closely matched the two struggling ants were in size, the longer they struggled. Related are the findings of Anderson and Jadin (2001) who showed that in *A. colombica* leaf transfer, post-transfer transportation speeds were significantly faster than pre-transfer, matching those of material not transferred. In other words, transfer appears to occur most often when transportation speed would be enhanced.

A simulation model

Whereas the above argument suggests that self-organised sorting should occur, the following computer simulation (320 lines of 'C' code) demonstrates the process in practice and also illustrates its dynamics. The assumptions exactly follow those of the argument above, however we state them explicitly here. We assume for simplicity and clarity that a large pile of seeds exists at position 0 on a trail and the nest is located at distance 1. When an ant arrives at the seed pile it instantaneously picks up a single seed from the pile (which supplies seeds *ad libitum*) and turns to start transportation of the seed to the nest. Any laden ant will always be travelling in the direction of the nest and any unladen ant will always be travelling towards the seed pile. When an ant arrives at the nest, it instantaneously drops its seed and turns to travel back down the trail.

When an unladen and laden ant meet on the trail, transfer may occur depending upon the relative transportation ability, i.e. speed, of the two ants: if the laden ant perceives that the unladen ant is larger, perhaps as a result of a (instantaneous) tug-of-war as in *M. barbarus*, and thus can transport the seed faster, then the seed is transferred. After any such transfer the now unladen ant sets off back towards the seed pile while the now laden (larger) ant transports the seed towards the nest. No interaction occurs between two laden or two unladen ants that happen to meet on the trail. Faster moving ants may overtake slower moving ants.

We consider two model variants:

a) *Monomorphism*: we assume a monomorphic population of ant workers in which there is continuous variation about some mean size, and hence transportation speed. Thus, this incorporates species that range from those with little interindividual differences to those with linear allometry and large interindividual differences (e.g., Wheeler 1991). We assume that all ants can detect small interindividual differences when they meet: if the laden ant's transportation speed is less than the unladen ant's transportation speed, then transfer occurs.

b) *Polymorphism*: we assume a polymorphic population of ant workers in which the ants are divided among c distinct castes, and hence speeds. We further assume that ants cannot detect small interindividual differences, i.e. detect any differences within their own caste, but only detect differences among castes. Thus, transfer only occurs if the unladen ant is from a larger, and therefore faster, caste than the laden ant.

At the start of each simulation, the ants are randomly distributed along the trail, and with probability 0.5 given a seed to transport, thus determining their initial direction of travel. Each ant is assigned a running speed from some given distribution. As this is an illustrative simulation only, we restrict ourselves to distributions with a mean running speed of 0.5 and use uniform distributions $U({}^1/_2 - x, {}^1/_2 + x)$ where $x < {}^1/_2$ for the monomorphic cases and a set of positive real values $v_1 < v_2 < \ldots < v_c$, i.e. $\{{}^1/_2 - 2y, {}^1/_2 - y, {}^1/_2, {}^1/_2 + y, {}^1/_2 + 2y\}$ where $y < {}^1/_4$, for the polymorphic cases. The distributions used are listed in Table 1. These speeds are a constant for each ant throughout the simulation and there is no difference between laden and unladen running speeds (as hinted at in the previous subsection, we can relax this assumption without affecting the results qualitatively). Thus, apart from the stochastic initial conditions, each simulation is deterministic and runs in continuous time.

Figure 2 demonstrates self-organised sequencing of individuals from slowest to fastest along the trail. After every 25 simulation "events," an event being when two ants meet or pass each other on the trail, a scan was made along the trail from source to nest. As each ant was encountered in the scan (except the ant nearest the nest), its speed was compared with the next downstream ant, with a dot representing correct sequencing (downstream ant is faster) and an 'X' representing a slower ant immediately downstream. Thus, figure 2 clearly shows that at the *global* level the group of ants was "correctly" sequenced, a property that emerges solely by simple local interactions – larger ants win fights over seeds – at the individual level.

This sequencing occurs rapidly (3.41 time units), faster than it would have taken an average ant (speed 0.5) to complete one whole round trip if working alone (2 × trail length/speed = 4 time units). This demonstrates that the self-sequencing proceeds quickly. It does not indicate, and indeed is not relevant to, which scheme processes seeds faster. Table 1 shows that the duration of this sequencing strongly depends upon the distribution of running speeds; that is, the wider the range of running speeds, the slower the mean sequencing time. This is to be expected because the speeds of the slowest ants are likely to be limiting, especially if they are initially positioned close to the nest – i.e., the other ants self-sequence while the "slowcoaches" amble to their correct position close to food source. More generally, the expected minimum of n deviates from $U(a, b)$, where $0 < a < b < 1$, is $a + (b - a)/(n + 1)$. For example, when 10 running speeds are drawn from $U(0.2, 0.8)$ the expected minimum is 0.254. Analysing the data in Table 1, we find a highly significant positive relationship between the reciprocal of the observed mean sequencing time (y, a crude measure of minimum speed) and the expected speed of the slowest ant (x, from the formula above) ($y = 1.45x - 0.058$; $r^2 = 0.953$; $F = 120.76$; $p < 0.0001$) thus supporting the idea that the slow ants are indeed limiting the speed of sequencing.

With polymorphic ants (2 ants of each of 5 castes, see Table 1), the same self-sequencing process occurs (results not shown) – thus generating the testable prediction that castes would be separated by distance along the trail. Complete self-sequencing is achieved after a comparable amount of time to the monomorphic cases. As with monomorphic ants, there is a highly significant relationship between the speed of the slowest ant (given in Table 1) and the reciprocal of sequencing time ($y = 1.09x + 0.106$; $r^2 = 0.994$; $F = 946.8$; $p < 0.0001$), again supporting the idea that the slow ants limit the sequencing time. Note, however, that the slopes of the two fitted equations are different, implying that slow ants are relatively less of a delay-factor in polymorphic workers, and that also the rate of self-sorting to be gained by increasing the speed of the slowest ant is less in polymorphic workers.

Both the verbal logic and the simulations show that patterns similar to size-sorted BBs may arise almost instantaneously if social insect workers are somehow constrained to operate with a simple "grab any food item you can" decision

Table 1. The mean time ("sequencing time", in bold, with their standard errors, in parentheses) until a set of 10 ants, with running speeds drawn from a given distribution, are first (self)sequenced from slowest (nearest the source) to fastest (near the nest). Note that every running speed distribution in the table has the same mean, 0.5, and that the variance of the two distributions within each row of the table are equal, e.g. $U(0.20, 0.80)$ and {0.255, 0.378, 0.5, 0.622, 0.745} both have mean 0,5 and variance 0.03. Results are based upon 100 replicates.

Variance of running speeds	Monomorphic ants		Polymorphic ants	
	Running speed distribution	Sequencing time	Running speed distribution	Sequencing time
6.75×10^{-2}	$U(0.05, 0.95)$	**12.74** (0.36)	{0.133, 0.316, 0.5, 0.684, 0.867}	**4.16** (0.17)
5.33×10^{-2}	$U(0.10, 0.90)$	**3.88** (0.19)	{0.173, 0.337, 0.5, 0.663, 0.827}	**3.66** (0.11)
4.08×10^{-2}	$U(0.15, 0.85)$	**3.12** (0.14)	{0.214, 0.357, 0.5, 0.643, 0.786}	**2.96** (0.10)
3.00×10^{-2}	$U(0.20, 0.80)$	**2.69** (0.091)	{0.255, 0.378, 0.5, 0.622, 0.745}	**2.60** (0.087)
1.33×10^{-2}	$U(0.30, 0.70)$	**2.20** (0.064)	{0.337, 0.418, 0.5, 0.582, 0.663}	**2.04** (0.067)
3.33×10^{-3}	$U(0.40, 0.60)$	**1.78** (0.045)	{0.418, 0.459, 0.5, 0.541, 0.582}	**1.76** (0.041)
8.33×10^{-4}	$U(0.45, 0.55)$	**1.64** (0.032)	{0.459, 0.480, 0.5, 0.520, 0.541}	**1.66** (0.035)
3.33×10^{-5}	$U(0.49, 0.51)$	**1.61** (0.024)	{0.492, 0.496, 0.5, 0.504, 0.508}	**1.58** (0.030)

```
Time  Source→Nest   0.90  S...XXX.X.N   1.88  S....X....N   2.95  SX........N
0.02  S.XX.XX.X.N   0.98  S...XXX..XN   1.90  S....X....N   3.02  SX........N
0.05  S.XX.XX.X.N   0.99  S...XXX..XN   1.93  S....X....N   3.05  SX........N
0.07  S.XX.XX.X.N   1.05  S....XX..XN   1.99  S.....X...N   3.06  SX........N
0.07  S.XX.XX...N   1.05  S....XX..XN   2.01  S.....X...N   3.13  SX........N
0.07  S.XX.XX...N   1.05  S....XX...N   2.04  S.....X...N   3.17  SX........N
0.10  S.XX.XX...N   1.08  S...X.X...N   2.05  S.....X...N   3.19  SX........N
0.13  S.XX..X...N   1.09  S...X..X..N   2.06  S.....X...N   3.22  SX........N
0.13  S.XX..X...N   1.10  S..XX..X..N   2.07  S....X....N   3.23  SX........N
0.13  S.XX..X...N   1.14  S..XX..X..N   2.11  S....X....N   3.29  SX........N
0.17  S.XX..X...N   1.21  S..XX..X..N   2.12  S...X.....N   3.29  SX........N
0.22  S.X.X.X...N   1.23  S..XX..X..N   2.15  S...X.....N   3.30  SX........N
0.25  S.X.X.X...N   1.28  S..XX.X...N   2.23  S...X.....N   3.34  SX........N
0.27  S.X.XX.X..N   1.29  S..XX.X...N   2.24  S...X.....N   3.36  SX........N
0.33  S.X..X.X..N   1.33  S...X.X...N   2.29  S...X.....N   3.41  S.........N
0.35  S.X..X..X.N   1.33  S...X.X...N   2.29  S..X......N   3.47  S.........N
0.35  S.X..X...XN   1.34  S...X.X...N   2.33  S..X......N   3.47  S.........N
0.36  S.X..X....N   1.38  S...X.X...N   2.33  S..X......N   3.51  S.........N
0.40  S.X..X..X.N   1.45  S..X..X...N   2.40  S..X......N   3.55  S.........N
0.45  S.X..X..X.N   1.47  S.....X...N   2.41  S..X......N   3.57  S.........N
0.49  SX.X.X..X.N   1.49  S.....X...N   2.46  S.X.......N   3.61  S.........N
0.49  SX.X.X.X..N   1.51  S.....X...N   2.49  S.X.......N   3.64  S.........N
0.50  SX.X.X.XX.N   1.51  S......X..N   2.55  S.X.......N   3.68  S.........N
0.51  SX.XX..XX.N   1.52  S......X..N   2.57  S.X.......N   3.73  S.........N
0.51  SX.XX..XX.N   1.53  S......X..N   2.59  S.X.......N   3.74  S.........N
0.51  SX..X...X.N   1.53  S......X..N   2.63  S.X.......N   3.78  S.........N
0.53  SX..X..X..N   1.62  S......X..N   2.65  S.X.......N   3.79  S.........N
0.53  SX..XX.X..N   1.63  S......X..N   2.66  SX........N   3.82  S.........N
0.53  SX..X.X...N   1.64  S......X..N   2.71  SX........N   3.90  S.........N
0.55  SX..XXX...N   1.68  S......X..N   2.72  SX........N   3.92  S.........N
0.55  SX..XXX...N   1.68  S......X..N   2.76  SX........N   3.96  S.........N
0.71  SX..XXXX..N   1.70  S.....X...N   2.84  SX........N   3.97  S.........N
0.71  SX...XXX..N   1.72  S.....X...N   2.84  SX........N   3.98  S.........N
0.71  SX...XXX..N   1.75  S.....X...N   2.87  SX........N   4.03  S.........N
0.71  S....XXX..N   1.77  S.....X...N   2.88  SX........N   4.04  S.........N
0.74  S...X.XX..N   1.78  S.....X...N   2.88  S.X.......N   4.04  S.........N
0.77  S...XX.X..N   1.83  S....X....N   2.90  S.X.......N   4.07  S.........N
0.80  S...XX.X..N   1.83  S....X....N   2.90  S.X.......N   4.07  S.........N
0.88  S...XXX.X.N   1.86  S....X....N   2.93  SX........N
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Figure 2. Demonstration of self-organised sequencing from slowest to fastest. Each line represents a scan along the trail from source (S) to nest (N) comparing each ant encountered with the running speed of the next downstream ant. If the downstream neighbour is faster than the focal ant, i.e. "correctly" sequenced, a dot is shown. If however, the adjacent downstream ant is slower, i.e. "incorrectly" sequenced, then an **X** is shown. Thus, at 3.41 time units the ants are first sequenced from slowest to fastest, i.e. a complete row of dots, and this sequence is maintained thereafter. Parameters: 10 ants, monomorphic population drawn from $U(0.15,0.85)$, trail length = 1. Results show the state of the system after every 25 "events," an event being when two ants meet or pass each other on the trail. The thick black line indicates the point at which an average ant (speed 0.5) would have completed one whole trip from source to nest and back to source if working alone, i.e. 4. This demonstrates only that sorting is achieved quickly

rule. This implies that it may be hard to judge from field data whether observed BBs represent an optimal foraging strategy according to the unconstrained colony-level cost-benefit criteria outlined in the first theoretical section, or a – not necessarily optimal – byproduct of a fixed decision rule that is adaptive for individual foraging.

Discussion

This study considers a particular form of task partitioning, bucket brigades, known to exist in insect societies, albeit rarely. BBs, which we define strictly for the first time, have both their advantages and disadvantages and our analysis above suggests that there may be ecological conditions in which BBs are favoured over other transportation schemes. The dominant conditions favouring BBs are likely situations in which:

1) it is difficult to pass each other on a trail, e.g. thin branches in a tree canopy or narrow tunnels;
2) performance efficiency may be increased by specialising upon a section of trail, a situation which arises naturally in BBs. (This is provided that unpredictable disturbances do not occur too frequently.) For instance, Wehner et al. (1983) report that familiarity with a foraging area can reduce the probability that an ant will get lost;
3) trails are long to enable any performance efficiency gains to be capitalised on;
4) transfer delays are short; these delays are likely to be longer with liquids than solids (Ratnieks and Anderson, 1999a) but even so transfer delays with solids could be significant.

This list suggests that ergonomically optimal BBs are most likely to occur in the transfer of solid items over long, narrow, and well-protected trails. This combination of transport characteristics is probably most common in underground trails and corridors, of which, unfortunately, relatively little is known (but see Weissflog et al., 2000; Anderson and McShea, 2001a). BBs may also be expected in ants that forage on narrow arboreal trails. Here, compared to underground trails, the higher risk of biotic disturbances from predators, parasites, and competitors, might be offset by an increase in trail fidelity. That is, when wind shifts branches and alters foraging trail odours, BBs have the advantage of restricting each worker to a shorter section of the trail thus making it more likely for an individual to be able to *remember* the correct route. It is perhaps no surprise, therefore, that several of the rare observations on BBs involve underground termites and leafcutter ants (discussed earlier). In all of these documented or predicted cases, we expect BBs to be expressed facultatively, i. e. expressed only under the above-defined set of conditions and to be replaced by another type of foraging as soon as, for example, trails widen. One aspect that we have not covered is that ant's assessments of relative size, especially if two individuals are closely-matched, may be error prone. As such, an ant receiving a load might soon find herself overburdened. One option open to her is to cache the material on the ground for collection by another (faster) individual (c. f. Anderson and Jadin, 2001). Thus, the error rate will certainly affect the expression of bucket brigades versus other forms of task partitioning.

Our simulations illustrate an important point about optimality in foraging: one should exercise caution when claiming that a particular transportation scheme is optimally organised, unless direct evidence about the group's maximand (i.e., maximised currency) confirms that a particular strategy is optimal at the colony-level. The apparent behaviour of our model-ants, i. e. sequenced from slowest to fastest, exactly matches that expected from dynamical systems theory (Bartholdi and Eisenstein, 1996; Bartholdi et al., 1999). That is, when there are blocking delays it can be proven mathematically that this slowest to fastest sequencing is a *globally-optimal* way of arranging individuals in a BB (Bartholdi et al., 1999) which maximises throughput (= seed "processing" rate). Our simulations show that such worker size-sorting process can happen very rapidly so that it may be encountered in the field even if only as a suboptimal transient state between individual foraging and a BB. Situations in which this might occur include 1) at a sudden narrowing of a trail, e. g. a narrow branch being the only possibility to cross a stream, and 2) with moderate resistance of smaller workers towards giving up their load. The latter behaviour would be selected for in species where BBs are almost never optimal, but where encounters with conspecific or allospecific competitor ants on the trails would be frequent enough to make "resistance until nestmate recognition" an adaptive strategy. The study by Reyes and Fernández (1999) is illustrative in this respect. It is tempting to draw the conclusion that *Messor* workers are acting in an optimal, and therefore efficient, manner. However, the fact that laden ants were apparently reluctant to give up their seeds suggests that part of the "joint handling times" created by this behaviour are inefficient and that an optimal looking sequence may have emerged spontaneously from self organised dynamics. The decision rule: "*if you are without a food item, run out along the foraging trail until you encounter one and then take it if you can, even if you must wrest from another ant, and carry it back towards the nest*" may only result in actual BB-like takeovers when trails are constrained beyond some narrowness threshold where blocking delays become significant. The fact that the ants operate with a decision rule based on normal individual foraging would then imply that BBs are established somewhat earlier than when they would be efficiency maximizing. The *Messor* study by Reyes and Fernández (1999) may represent such a situation.

The crucial point seems to be to separate the causes of size-sequencing and BBs. With a monomorphic worker caste, it seems reasonable to expect that BBs may be close to an optimal task partitioning device when they are observed regularly. This expectation should then be tested by comparative observations on running speed, transfer delays, and blocking delays to understand where the decisive payoffs selecting for this behaviour arise. However, in species with a polymorphic worker caste, it seems essential to find out whether joint handling delays are a function of the worker size difference and whether these delays represent an extra cost that might make the BB less efficient than it otherwise could have been. However, it is important to note that further complications may prevent detailed optimality tests of BBs.

We should stress that absolute transportation speed may not always be the currency that is being maximised. This is because transfer, whether direct or indirect, may also have additional and hard-to-measure payoffs. For example, BBs may be a way of transferring information between individuals about what is being collected and may have a positive effect upon recruitment and trail reinforcement (e. g. see Varjú and Núñez, 1991; Núñez, 1982; Roces and Núñez, 1993; Núñez and Giurfa, 1996). With task partitioning, during the initial phases of exploration and recruitment a scout can quickly return to the foraging site and reinforce the trail. Röschard and Roces (2001 and pers. comm.) conclude that this is the likely benefit of multistage partitioning in *Atta vollenweideri* – in a laboratory study, they found that the highest frequency of BBs formed at high quality sites – and this has also been suggested for other *Atta* species (Hubbell et al., 1980; Ratnieks and Anderson, 1999 a).

BBs may thus arise without being absolute efficiency maximizing devices or they may be more optimal than they seem for additional hard-to-quantify reasons. However, it seems unlikely that any BB observed in nature would be truly maladaptive because we should then expect that the expression of this behaviour would be suppressed by natural selection. The level of selection is important: in highly cooperative and related groups such as insect societies, behaviour or costs which may appear somewhat maladaptive and suboptimal at the individual level, can be highly adaptive and beneficial at the colony level when viewed on a longer timescale. For instance, at first sight, losing a foraging trail – which in some ants occurs with a constant probability per unit time (e. g. Deneubourg et al., 1983, 1987) – would seem maladaptive for a lost worker and for the colony. Although some of these lost ants may die, be predated and so on, importantly, some may find new food sources, return to the nest and recruit others to their finds. It seems that this may well be an optimal colony level strategy that allows a colony to continue to exploit known food sources, using the ants that do not get lost, while searching for new sources, using the lost ants. As such it becomes meaningful to speak of "adaptive error" (Deneubourg et al., 1983, 1987; Weidenmüller and Seeley, 1999), a concept absent from classical optimal foraging theory (e.g., absent from Parker and Maynard Smith's 1990 review). In short, when talking about optimality of cooperative foraging and transportation schemes, don't judge a book by its cover. Details matter and perhaps in *Messor* such seemingly "suboptimal" behaviour is adaptive in some other way. In conclusion, we present a mixed message about BBs and the extent of their optimality: just because something looks optimal, e.g. size-sorted sequencing, it does not necessarily mean it is maximally efficient. Conversely, just because something looks inefficient and suboptimal, e.g. long joint handling times, it does not necessarily mean it is selected against. That is, there may be unknown or unmeasured benefits at play, or the trait may be expressed rarely and only as a byproduct of individual decision rules that make the system maximally efficient under "normal" foraging. Ydenberg and Schmid-Hempel (1994: p. 491) state that "whether individuals [do] sacrifice their own foraging efficiency in favour of colony performance is unclear, as theory and experiment have not yet properly addressed these issues." This is certainly true of BBs; more detailed research is clearly needed.

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