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Optimality in a partitioned task performed by social insects

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Biologists have long been aware that adaptations should not be analysed in isolation from the function of the whole organism. Here, we address the equivalent issue at the scale of a social insect colony: the optimality of component behaviours in a partitioned sequence of tasks. In colonies of *Atta colombica*, a leaf-cutting ant, harvested leaf tissue is passed from foragers to nest workers that distribute, clean, shred and implant the tissue in fungal gardens. In four laboratory colonies of *A. colombica*, we found that the highest colony-wide rate of leaf tissue processing in the nest was achieved when leaf fragment sizes were suboptimal for individual delivery rate by foragers. Leaf-cutting ant colonies appear to compromise the efficiency of collecting leaf tissue in order to increase their ability to handle the material when it arrives in the nest. Such compromise reinforces the idea that behavioural adaptations, like adaptations in general, must be considered within the context of the larger entity of which they are a part.

Keywords: adaptation; *Atta colombica*; foraging; leaf-cutting ant; optimality; task partitioning

1. INTRODUCTION

Questions about optimality are of central importance in understanding how natural selection shapes adaptations (Crespi 2000; Orzack & Sober 2001). In their famous critique of adaptationism, Gould & Lewontin (1979, p. 585) warned against atomizing organisms and evaluating the optimality of the parts in isolation. At the same time they objected to invoking trade-offs so that 'suboptimality of a part is explained as its contribution to the best possible design for the whole'. Yet trade-offs seem inherent to the interaction of components that contribute to the good of a larger entity. These issues, originally argued with respect to whole organisms, apply equally to supraorganismal entities such as social insect colonies, and to behavioural as well as morphological adaptations.

In many social insect colonies, the organization of work involves task partitioning in which a sequence of material handling is carried out by different individuals (Ratnieks & Anderson 1999). Here we consider the optimality of a partitioned foraging task in colonies of *Atta colombica*. Load size affects a worker's individual rate of resource harvesting because of the time it takes to cut a leaf fragment (Wilson 1980a;

Van Breda & Stradling 1994) and because load size affects the walking speed of returning ants (Lighton *et al.* 1987; Burd 2000a, 2001). Like other leaf-cutting ants, *A. colombica* foragers cut fragments of plant tissue and carry the loads to their subterranean nest, where the tissue is used to cultivate fungal gardens to feed the colony's larvae. *Atta colombica* foragers range from approximately 3 to 30 mg in body mass, and smaller workers tend to carry smaller leaf fragments (Burd 2000a). Previous investigation has shown that *A. colombica* foragers of all sizes nearly always carry loads that are smaller than needed to maximize their individual rate of tissue delivery to the nest (Burd 1996, 2000a, 2001). For example, workers of average size would need to carry 35 mg fragments (approx. 175 mm² for leaves with a typical density of 0.20 mg mm⁻²) in order to maximize their own delivery rate (Burd 1996). But *Atta* foragers nearly always carry loads well below this size, usually about 20 mg or less (Howard 1991; Burd 1996, 2000b).

We have argued that this apparently suboptimal behaviour must be understood in the context of task partitioning (Burd & Howard 2005a,b). When foragers deliver harvested leaf tissue to the nest, the fragments are distributed by other workers to hundreds of fungal gardens, where still other workers clean and dissect them to tiny particles, which are then implanted among the garden hyphae (Weber 1972; Wilson 1980b). Inefficient delivery of small fragments by foragers outside the nest might be explicable if small fragments are transported and processed inside the nest more rapidly (Burd & Howard 2005b).

Here we provide experimental support for this hypothesis. We measured the ability of four laboratory colonies of *A. colombica* to incorporate leaf tissue into their fungal gardens when the tissue was supplied in leaf fragments of a particular size ranging from the abnormally tiny to the abnormally large. Intermediate leaf fragment sizes, near the mean size actually harvested by colonies in the field, produced superior performance inside the nests of all four colonies.

2. MATERIAL AND METHODS

The four colonies were obtained near Gamboa, Republic of Panama, in 1998 and kept at ambient conditions in a laboratory at the University of New Orleans. The colonies were provided a variety of local woody plants, including the species used for the experiments reported here. Nests were constructed of three 2.5 l boxes of transparent plastic, connected serially by 100 mm lengths of tubing with an internal diameter of 20 mm. These dimensions are similar to those of tunnels and garden chambers in natural *Atta* nests (Weber 1972). The most 'upstream' nest-box led to an open, Fluon-lined 10 l foraging arena, and the most 'downstream' box led to a refuse dump. One colony had three small fungal gardens in each chamber, two colonies had fungal gardens in the central and downstream boxes, and one had a single garden in the central box. We estimated garden size by the product of the longest length, width, and height of each garden. The four colonies had approximately a fourfold range of total garden sizes (table 1).

In each trial, we introduced a known number of leaf fragments of a uniform size into the most upstream chamber of each colony, after it had been deprived of leaf tissue for 12–16 hours. The fragments were circular discs in the range 11–209 mm² cut from the lamina (but avoiding the midrib) of freshly gathered leaves of white mulberry (*Morus alba*, density 0.12 mg mm⁻²) or Chinese tallow (*Sapium sebiferum*, density 0.14 mg mm⁻²). The resulting aggregate of fragments resembled the caches that accumulate naturally when influx exceeds the colony-wide processing rate (Hart & Ratnieks 2000). We replenished the cache with a known number of fragments whenever it neared depletion, over periods that ranged from 3 to 7 hours.

We allowed the colonies to transport the fragments downstream and incorporate the tissue into their fungal gardens. We measured

Table 1. Regression analysis of fragment flux as a function of disc size. (Flux, r , in number of discs h^{-1} ; disc area, A , in mm^2 .)

colony	total garden size (cm^3)	flux of fragments	F	d.f.	p -value	r^2
24	739	$\ln r = 4.87 - 0.0196A$	139	1,4	0.0003	0.97
41	1498	$\ln r = 3.80 - 0.0196A$	515	1,3	0.0002	0.99
29	2067	$\ln r = 5.47 - 0.0169A$	90	1,8	0.00001	0.92
54	2937	$\ln r = 5.44 - 0.0105A$	81	1,9	0.000006	0.90

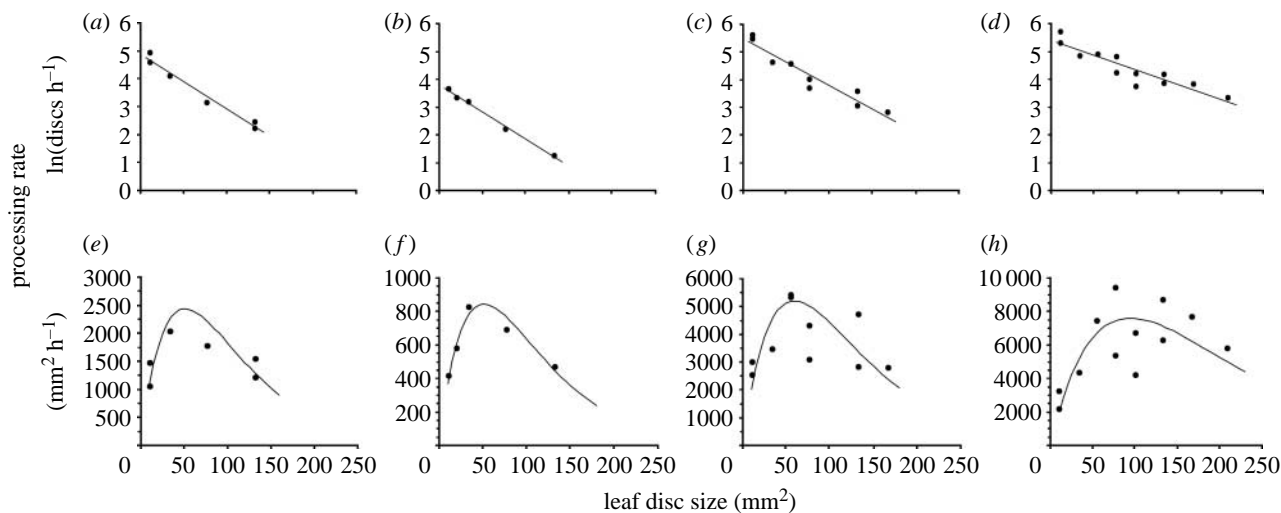


Figure 1. (a–d) Colony-wide flux of fragments in individual trials as a function of fragment size. Equations and statistics of the regression lines shown are given in table 1. (e–h) Data and regression lines in (a–d) translated to area-specific rates. (a, e) Colony 24, (b, f) colony 41, (c, g) colony 29, (d, h) colony 54. Colonies are ordered left to right by increasing total garden size.

the duration of the process from the first introduction of leaf discs into the cache until the dissection of the last disc on any of the colony's gardens. (A variety of alternative measures of duration, such as time until dissection of the penultimate disc, or the mean time until the last piece of leaf tissue was implanted among the hyphae in individual gardens of a colony, produced quantitatively very similar results.) From the total number of discs introduced in each trial and the time required to process them, we calculated the colony-wide rate of leaf tissue processing.

3. RESULTS

The smallest leaf discs were rapidly transported, cleaned and dissected, but because these discs contained little tissue, the net colony-wide processing rate was low in all colonies. The largest discs that workers could transport (from 135 to 209 mm^2 , depending on the colony) contained more tissue in each one, but they were transported and handled so slowly that the net rate was again quite low. Intermediate sizes yielded the best collective performance.

The colony-wide flux of fragments (total number of discs processed divided by total processing time) declined approximately exponentially with disc size in each of the colonies, as indicated by linear relationships between the logarithm of the flux and disc size (figure 1; table 1). The regression equations for these relationships, in the form $\ln r = k - bA$, with r in units of discs h^{-1} and disc area A in mm^2 (table 1), are algebraically equivalent to $r_A = A \cdot \exp(k - bA)$, that is, with the colony-wide processing rate expressed in $\text{mm}^2 \text{h}^{-1}$. In these units, the processing rates have nonlinear relationships to fragment size, with the maximum rate at $A = 1/b \text{ mm}^2$ (figure 1). For the regression parameters estimated in table 1, the maximal colony-wide rates are predicted to occur at leaf fragment sizes of 51, 51, 59 and 96 mm^2 among

the four colonies, with the smaller optima for the colonies with smaller gardens.

4. DISCUSSION

These results are consistent with the argument that what is suboptimal at one level can be optimal at a different, more inclusive level. The optimal fragment size of 96 mm^2 that we determined here for the largest laboratory colony (figure 1) compares well with the mean fragment sizes actually harvested by *Atta* colonies in the field: 93 mm^2 for fragments harvested by 11 *Atta cephalotes* colonies in Costa Rica (Wetterer 1994); 72, 93, 94, 97 and 123 mm^2 for five *A. cephalotes* colonies in Costa Rica (Burd 2000b); 86.3 mm^2 for 49 *A. colombica* colonies in Panama (Wirth *et al.* 2003). These values are larger than the optima for our other three laboratory colonies. But to make this comparison, we should account for the smaller size of the workers in the laboratory colonies relative to wild colonies. The foragers in the laboratory colonies had a mean body mass of $4.8 \text{ mg} \pm 3.1$ s.d. ($n = 103$), while the mean body mass of laden *A. colombica* foragers sampled in Gamboa, Panama (the source of our colonies) was $8.5 \text{ mg} \pm 3.8$ s.d. ($n = 506$; J. J. Howard 1998, unpublished data): almost a twofold difference. If we restrict this Panamanian field sample to workers up to 8.8 mg and to those carrying leaves with a density of $0.15\text{--}0.20 \text{ mg mm}^{-2}$ (still above the density used in our experiments), the mean load mass was $9.7 \text{ mg} \pm 5.0$ s.d. ($n = 120$), equivalent to mean fragment areas of approximately 48–65 mm^2 , quite similar to the optima for the three smallest colonies (figure 1). Those foragers up to 8.8 mg from five *A. cephalotes*

colonies in Costa Rica, cutting leaves of $0.13\text{--}0.30\text{ mg mm}^{-2}$, took fragments with mean areas of $65\text{--}106\text{ mm}^2$ (Burd 2000b), similar to the complete range of optima in figure 1.

Although these mean values from the field are consonant with our results, there is substantial variation in the size of harvested fragments, corresponding to the polymorphism of foragers. This variation may have a functional value. Because small fragments are transported more easily and rapidly inside a nest (Burd & Howard 2005a), they may be distributed preferentially to the most remote fungal gardens, while larger fragments are used in gardens nearer to the nest entrance. Small fragments may also allow a colony to shift resources rapidly in response to transient shortages in some chambers, satisfying the most urgent need and thus raising the productivity in all chambers. At present, however, there have not been any quantitative studies of the internal dynamics of leaf tissue transport in field colonies of *Atta*.

Partitioning of tasks is known to enhance ergonomic efficiency of the whole colony in ants and other insect societies (Jeanne 1986; Anderson & Ratnieks 1999). Our results show that *Atta* colonies can maximize the flow of resources into their fungal gardens if the leaf fragments they handle are too small to optimize the performance of the foragers that harvest and deliver them. Thus, the function of the components of a partitioned task may not be comprehensible when viewed in isolation, much as Gould & Lewontin (1979) warned that individual adaptations should not be assessed apart from in the context of the whole organism. But their insistence that suboptimality of component parts does not contribute to optimality of the whole seems incorrect. We have shown that *Atta* colonies can operate at or near an ergonomic optimum, albeit a complex optimum that is not necessarily apparent when the component tasks are examined in isolation. Much of the uncertainty over the adaptive value of foraging behaviour in *Atta* ants (Wilson 1980a; Howard 1991; Wetterer 1991; Roces & Núñez 1993; Burd 2000b) seems resolvable with this perspective.

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