Behav Ecol Sociobiol (2017) 71: 14
DOI 10.1007/s00265-016-2237-5

ORIGINAL ARTICLE

Energetics of trail clearing in the leaf-cutter ant *Atta*

Thomas Bochynek[1,2,3] · **Bernd Meyer**[1] · **Martin Burd**[2]

Received: 13 July 2016 / Revised: 8 October 2016 / Accepted: 13 November 2016 / Published online: 7 December 2016

Abstract
Few ant species construct cleared trails. Among those that do, leaf-cutting *Atta* ants build the most prominent networks, with single colonies clearing debris and obstructions from hundreds of meters of trails annually. Workers on cleared paths move at higher speed than they do over uncleared litter, and one measurement of the time and energetic costs of trail clearance suggests that benefits of trail usage far outweigh the investment costs of trail clearing. The ecological basis of trail clearing remains uncertain, however, because no full account has been made of benefits and costs in common units that allow comparison. We make such an account using a scalable, integrative model of trail investment and foraging energetics. Contrary to assumptions in previous work, we find that trail clearing needs not always be energetically profitable for leaf-cutting ants. Profitability depends on the workforce composition, specifically, on how many ants in a traffic stream act as maintenance workforce to respond to sudden and unpredictable obstructions, such as leaf fall. Such maintenance patrols have not previously been recognized as a cost of trail building. If the patrolling workforce is not too large, the energetic savings from foraging over cleared trails offset the investment and maintenance costs within a few days. Under some conditions, however, amortization can take weeks or months, or trail clearing can become unprofitable altogether. This suggests that *Atta* colonies must have a mechanism to regulate the intensity of their trail clearing behavior. We explore possible mechanisms and make testable predictions for future research.

Significance statement
Leaf-cutter ants build prominent, cleared trails of up to 200 m length through rainforest undergrowth. Construction of such trails appears costly, yet little is known about the energetics of cleared trails. No research exists on the benefits of their use, and only a single case study investigated parts of the construction costs. While this case study concludes that trail clearing is "relatively inexpensive," we argue that it failed to include a deciding factor in the cost/benefit analysis: the cost of providing a standby clearing workforce, which is distinct from the foraging workers. We construct a full, scalable cost-benefit model from our own empirical measurements and literature. Contrary to previous results, we find that trail clearing is not always profitable, but profitability depends on the foraging conditions. This prediction offers a new perspective on the occurrence of uncleared trails in the field.

Keywords Cleared trails · Trunk trails · Leaf-cutter ants · Atta · Cost/benefit model · Unladen workers

Introduction

Ants are successful in large part because of their ability to cooperate in groups, accomplishing collectively far more than individuals could achieve alone. One of the most dramatic

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Communicated by W. Hughes

Electronic supplementary material The online version of this article (doi:10.1007/s00265-016-2237-5) contains supplementary material, which is available to authorized users.

✉ Thomas Bochynek
Thomas.Bochynek@monash.edu

[1] Faculty of Information Technology, Monash University, Melbourne, Australia

[2] School of Biological Sciences, Monash University, Melbourne, Australia

[3] CSIRO Data61, Canberra, Australia

examples of such collective achievement is the construction of cleared trails for foraging traffic. While most ant species rely on pheromone trails to guide their collective movements (Hölldobler and Wilson 1990), a small number of ant species build tangible trails cleared of undergrowth and organic debris, often down to bare soil—outstanding features of order in an otherwise unstructured environment. Cleared trails have been reported for species of *Atta*, *Formica*, *Lasius*, *Pogonomyrmex* (Hölldobler and Wilson 1990), *Messor* (Acosta et al. 1993; Plowes et al. 2013), *Camponotus* (Marlin 1971), *Iridomyrmex* (Greaves and Hughes 1974), and *Acromyrmex* (Gamboa 1975; Wetterer 1995). Most prominent among trail clearers are the New World leaf-cutter ants in the genus *Atta*. They remove large quantities of debris and vegetation by cutting obstructions with their mandibles and dragging or carrying the pieces from the path of traffic. Additionally, they shift soil or mill into the side of hill slopes to flatten trails (personal observation; also see Griffiths and Hughes 2010). This activity creates a transport infrastructure of greater dimension and higher quality than that of other collectively foraging species. Individual trails frequently extend more than 100 m and sometimes more than 200 m (Lewis et al. 1974a; Shepherd 1982; Wirth et al. 2003), and a single *Atta* colony may clear thousands of meters of trails over a year (an average of 2730 m/year for colonies of *Atta colombica* in the rainforest of Barro Colorado Island (BCI), Panama; Howard 2001). Such cleared trails connect the monodomous nests housing up to several million individuals (Villesen et al. 1999) to persistent feeding sites, from which foragers retrieve leaf fragments and other plant material as substrate for their symbiotic fungus (Hölldobler and Wilson 1990). These trails may be used for months and years (Howard 2001; Wirth et al. 2009). This intensity and extent of trail clearance seem to require a substantial energetic investment.

Shepherd (1982) hypothesized that the benefits of improved foraging through the ease and speed of movement (Rockwood and Hubbell 1987; Fewell 1988) and an increase in resource discovery rate (Shepherd 1982) along cleared trails would outweigh the costs of time and effort devoted to construction and maintenance of trails. In a case study with *A. colombica*, Howard (2001) explored this suggestion by making estimates of the annual energetic and time costs of trail construction. His estimates were based on observation of ants cutting and removing leaf litter from trails and measurements of leaf litter fall rates. Leaf removal required around 11,000 ant-days of effort, an annual energetic cost approximately equivalent to the intake of 8000 leaf fragments. Considering that colonies often field more than 10,000 foragers (Lugo et al. 1973; Howard 2001; Bruce and Burd 2012) at a given time, Howard concluded that the payback for trail clearing by an entire colony “can be accomplished in a matter of days” (Howard 2001).

These measurements, useful though they are, do not compare the energetics of trail construction against its alternative: what would happen if leaf-cutter ants did not clear their trails? Any adaptive advantage of *Atta* trails can be understood only in reference to the alternative of walking over forest floor litter to retrieve the same quantity of leaf fragments while avoiding the investment in trail clearance and maintenance. In the field, *Atta* colonies do indeed sometimes forage on uncleared trails. While this can be a temporary necessity (e.g., during the establishment of a trail to a new resource site or during collection of ephemeral, scattered resources like fallen fruit), other uncleared trails are used for weeks of foraging (personal observation). The use of such uncleared trails suggests that trail clearing may not be profitable under all conditions.

In our model, we explicitly compare the energetic payoff of foraging over cleared against uncleared trails. We can thus extend Howard’s work by providing a complete cost-benefit analysis that is independent of an individual case study and even allows us to assess hypothetical scenarios.

Our model also incorporates an aspect of trail clearance that has been previously overlooked. Long-term use of a trail requires continuous clearing of newly occurring obstructions. Howard (2001) considered only the immediate energetics of cutting and removing such obstructions from a trail, but not the cost to the colony of fielding the extra workforce to carry out these maintenance tasks. We postulate that maintenance requires more workers to be present on a trail than would otherwise be needed for foraging, defense, and other tasks. There are indications that these maintenance workers are partially distinct from other ants on foraging trails. Trail clearers tend to be larger than leaf-carrying foragers (about 15% greater head width, on average) but are rarely drawn from the largest workers, soldiers with head widths above 3.0 mm (Howard 2001). Laden workers do not readily drop their fragments to remove obstacles they encounter (personal observation), leaving trail clearing to be performed by unladen workers, as previously suggested by Lugo et al. (1973) and Lewis et al. (1974b). Ants marked during trail clearance display a higher probability than foragers of being recruited to experimental trail debris 24 h later (Howard 2001). Our observations of trail clearing in laboratory colonies of *Atta* suggest that about a quarter of the obstructions removed from the path are displaced by ants meandering on the trail outskirts rather than actively moving with the traffic stream (unpublished data).

Although trail clearers are statistically distinguishable from other workers, they are probably recruited to obstacles by known mechanisms of response thresholds (Theraulaz et al. 1998) from the pool of workers available on a trail and may return to other tasks after trail clearing. The time they spend clearing, however, must reduce the overall rate at which other tasks are performed throughout the trail. In order to redress the shortfall, a colony would need to field additional workers so that all tasks are performed at the desired rate, given the need for redundancy that probabilistic response thresholds entail (Herbers 1981). Moreover, a multi-tasking workforce sufficient to perform all other tasks at the needed rates would not be sufficient to maintain trails if trail clearance is the most demanding task. Colonies in the field seem capable, however, of rapid response to trail obstructions. Howard (2001) noted that clearing ants were recruited to experimental obstacles in a mean time of 123 s after placement of the obstacle on the trail, implying that a reserve of workers is available throughout the trail to respond to unpredictable need for clearance. It is difficult to estimate empirically how much the traffic stream of a colony is expanded to satisfy this need, but since laden ants do not generally remove obstacles, it is likely that some fractions of the unladen ants account for the additional capacity. In our model, we represent this fraction as a "clearing workforce" specified by an adjustable parameter that controls its size. We then explore variation in this parameter within the observed range of unladen ants in natural traffic flows. This new perspective highlights the need for research on the enigmatic presence of the large fraction of ants on a trail seemingly not performing any task.

We calculate both the costs and the benefits of trail clearing in a common energetic currency by drawing on a variety of published sources and our own measurements of movement on cleared and uncleared trails of field colonies of *Atta*. We use our model to examine how the energetic profitability of trail clearing changes with the length and usage of trails. We particularly investigate the effect of altering the proportion of unladen ants in the traffic stream and their contribution to a standby clearer workforce. We find that trail clearing costs can be recovered within a few days under many realistic foraging parameters but that there are also realistic conditions under which amortization takes weeks or months or is never achieved. We show that the composition of the workforce is one of the deciding factors in the cost/benefit balance, and we make predictions about behavior that are testable in the field.

Methods

We outline the conceptual structure of the model here, reserving full details for the appendix. Our strategy for calculating the energetic value of trail clearance is to estimate the metabolic expenditure due to all ant activity on a cleared trail and compare this to the total expenditure needed for an equal leaf harvest over an uncleared trail. Locomotion and load carriage will be less energetically demanding on a cleared trail, but the colony incurs the cost of clearing and maintaining the trail. In contrast, workers will expend more energy traversing an uncleared trail, but the colony avoids construction and maintenance expenses. The balance of these effects yields the net benefit of trail clearance to the colony

$$B(t) = E_{\mathrm{UC}}(t) - E_{\mathrm{C}}(t)\ [\mathrm{J}],$$

where B denotes the benefit in Joules; E the energetic cost of all worker activity on the trail including any clearance, outbound and inbound travel, and load carriage; subscripts UC and C represent uncleared and cleared trails, respectively; and t the duration of foraging (see Appendix B, Equation 7). The development of new trails carries an initial clearance cost, so the net benefit, B, starts out negative at $t = 0$ in our model. But if cleared trails deliver a net advantage, the energetic savings will accumulate as foraging progresses, so that the initial trail investment is recuperated and B eventually rises to zero. Further foraging on the trail then delivers a positive net benefit (Fig. 1). We use the time at which $B = 0$ (the "break-even time") as the measure of model performance in order to compare the effect of changing parameter values.

Components of trail clearing and maintenance

How much material must be removed to create a cleared trail? Howard (2001) measured standing leaf litter on the ground of the BCI rainforest and estimated that colonies of *A. colombica* remove approximately 1.22 kg of leaf litter per square meter of trail area during the initial construction of a trail. A similar amount of fresh litter fall, 1.44 kg, needs to be continuously removed from an existing trail over the course of a year (Leigh and Windsor 1982). Howard (2001) then measured the time cost (ant-hours) needed to cut and remove natural obstacles of known mass from active trails. He extrapolated these experimental measurements to the time investment needed to remove 1.22 or 1.44 kg of litter per square millimeters of trail surface and translated the time costs to energetic costs based on metabolic expenditures during leaf cutting and load carriage reported by Roces and Lighton (1995) and Lighton et al. (1987). We use these estimates of energetic cost directly in our model.

Howard's (2001) estimates refer to the direct metabolic costs of removing obstacles, but not the costs of making workers available to respond to unpredictable needs for trail

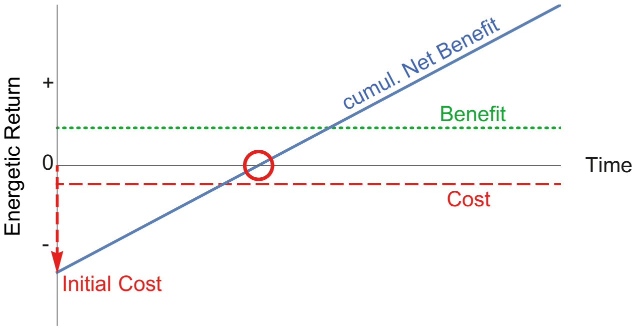


Fig. 1 Cost/benefit model concept. One-time initial clearing cost and continuous daily costs (indicated by *dashed line*) are amortized by the continued energetic savings of foraging on a cleared trail. Continuous costs are a combination of maintenance costs and the cost of patrolling standby clearers. As long as the energetic savings (indicated by *dotted line*) on a cleared trail outweigh the cost of keeping it cleared, a break-even point (indicated by *red circle*) is reached

maintenance at all times. We incorporate this cost in our model with a term representing a standby clearing workforce. As noted earlier, this workforce needs not exclusively perform trail maintenance and so need not be a completely distinct portion of the trail traffic. Nonetheless, the need for trail clearance would add to the workforce needed on the trail, and we account for the extra demand by adding a term in our model to represent the trail clearers as a fraction of the unladen ants occurring on the trail. The proportion of unladen workers observed on trails varies greatly from 13 to 80% of a traffic stream (Lutz 1929; Hodgson 1955; Cherrett 1968; Cherrett 1972; Lugo et al. 1973; Lewis et al. 1974a) (see Appendix A, Table 3). Not all of these unladen workers are necessarily standby clearers, but little comprehensive research exists on what function they perform. Bollazzi and Roces (2011) argue that during establishment of foraging traffic, workers return to the nest without carrying leaves to maximize recruitment speed, which would give some unladen workers a role in information transfer. The smallest unladen workers (referred to as "minims") are known to hitchhike on and clean leaf fragments during transport (Griffiths and Hughes 2010) and to play a role in pheromone trail maintenance (Evison et al. 2008). Littledyke and Cherrett (1976) noted that unladen workers aid in leaf-sap transport, and Da-Silva et al. (2012) observed water transport by unladen workers, although these observations came from a laboratory setting.

Thus, it is challenging to make informed estimates of the number of extra workers present on a trail due to the need for trail maintenance. We can, however, explore the range of possible variation up to the extreme point at which all unladen workers are taken to be a standby workforce for trail clearing. We represent this workforce with a model parameter u_S designating a fraction of the unladen ants on the trail and analyze how the energetics of trail clearing changes with this proportion.

Effects of cleared and uncleared trails on movement

The net benefit of clearing, if one exists despite the investment costs, would come from easier locomotion along a trail. That is, workers using an uncleared trail move more slowly and thus expend metabolic energy for a longer time on a given journey than they would if the trail was cleared. To measure this effect, we recorded the traffic of an *A. colombica* and an *Atta cephalotes* colony over cleared and uncleared portions of their foraging trails in April 2014. Each colony had a number of foraging trails that persisted during several weeks. We recorded 2-minute segments of traffic flow during peak foraging hours on three and four cleared segments and two uncleared segments of the trails of each colony, respectively. The cleared trails had been cleared down to the soil and featured no obvious obstructions. For uncleared trails, we only sampled sections of trails that showed no visible indication of leaf litter removal. From the recordings, we measured the time needed for randomly selected ants (529 in total) to cover 30 cm of trail length and calculated their speed. Because of the nature of the recordings, data extraction was nonblind. We found an approximately twofold greater speed on cleared trails than on uncleared trails (see Appendix A, Table 2 for averaged results, and electronic supplementary material for the full dataset). This is smaller than the suggested fourfold to tenfold increase reported by Rockwood and Hubbell (1987). The effect is likely to vary with the abundance and nature of the trail obstructions. A greater locomotion advantage of cleared trails would yield a greater energetic advantage in our model.

Translating movement to metabolic cost

In our model, a colony's energetic costs are calculated from the time used to perform various tasks, the cost of an individual ant undertaking it, and the number of ants performing them. As described above, we use Howard's (2001) estimates of metabolic expenditure per unit area of trail surface to account for activities directly involved in clearing vegetative litter from a trail. The other costs in the model come from locomotion between the nest and the foraging site by foragers, standby clearers, and other ants. Journey time is a function of speed, and individual workers may be unladen or laden with leaf fragments. The model calculations reported here assume that locomotion speed on a cleared trail is a function of ant size and load mass as reported for *A. colombica* by Burd (1996) and that speed on an uncleared trail is approximately half that on a cleared trail (see Appendix A, Table 2). We further assume that laden foragers carry leaf fragments related to their size according to the average loading pattern observed by Burd (1996) for *A. colombica* harvesting leaves of *Cordia alliodora*. These assumptions are well within the range of typical behaviors for *A. colombica* and *A. cephalotes* in tropical forest, but the model could be parameterized to represent other circumstances, such as the activity of grass-cutting *Atta* species that carry elongated fragments of grass leaves (Moll et al. 2012).

From walking speed, we then estimate metabolic expenditure. Lighton et al. (1987) measured oxygen consumption of *A. colombica* ants at rest and during locomotion and found that the rate of consumption per unit body mass rose linearly with speed. The net rate—consumption while walking less resting consumption—divided by walking speed yields the net cost of transport (NCOT), i.e., the volume of oxygen consumed in moving a unit mass a unit distance. Taking account of their measured scaling of NCOT with body mass and the well-established equivalence of body mass and external load mass on the cost of transport yields an expression for NCOT as a function of ant mass, load mass, and speed (Lighton et al. 1987, Eq. 16). Oxygen consumption can then be converted to Joules of metabolic energy (Lighton et al. 1987, Eqs. 3 and

11). See Appendix A for details of the calculation of metabolic costs.

Complete trail activity

The model represents the simple case of a single trail of length *l*, which may be completely cleared or completely uncleared (*Atta* colonies opportunistically exploit fallen branches, rocks, or other naturally exposed features as part of their trails). Howard's (2001) estimate of clearing costs accounted for such features as 9.3% of the total length of a trail, but Farji-Brener et al. (2007) found that naturally exposed branches made up 30% of the length of *A. cephalotes* trails in Costa Rica. For simplicity, we use Howard's (2001) estimates with their implied proportion of 9.3%, but other values could be modeled by simple adjustment of the clearing cost per unit of trail length. Ants on the model trail follow a body size distribution based on the measurements of Howard (2001), in which trail-clearing workers are about one third heavier than foragers (Appendix A, Table 1). The number of laden ants using the trail is estimated from the scaling of traffic flow with trail length reported for 18 *Atta* colonies in Costa Rica and Panama (Bruce and Burd 2012). The number of laden ants returning to the nest per minute scaled as a slightly superlinear function of trail length (scaling exponent = 1.28). We calculate the number of round trips per day needed to maintain these laden traffic flows, assuming 10 h of foraging per day and accounting for the typical daily rhythm of foraging activity (see Appendix B). For a 100-m trail, our model implies 6933 leaf fragments harvested per day.

Laden ants in the traffic flow are accompanied by unladen nest mates, which make up a fraction u of the total traffic. We explored a range of values for u from the lowest to highest values reported in the literature (Appendix A, Table 3). To account for unladen workers that might perform tasks not related to trail clearing, we introduce the parameter u_S to represent the fraction of unladen ants working as trail clearers. The fraction u_S has never been investigated empirically, as the potential energetic cost of trail clearers has not been recognized. We considered the full range of possible values from 0 to 1 for calculating model results. In particular, we searched for the parameters conditions under which trail clearing is or is not an energetically beneficial behavior and investigated the dynamics at the transition between these phases.

In sum, a given trail length in the model implies a certain number of laden and unladen round trips per day by ants of a certain size distribution. Ants move at speeds determined by their size and, if laden, the typical pattern of loading, and by the state of the trail, cleared or uncleared. The metabolic cost of round trips at these speeds is derived from the physiological measurements of Lighton et al. (1987), and the model thus calculates the total metabolic expenditure involved in all trail activity. A comparison of the energetic costs on cleared and uncleared trails yields the net benefit of clearing, B, as outlined above. We provide a detailed overview over all parameters and functions used in our model in Appendix A; the model structure itself is detailed in Appendix B.

Results

Despite the seemingly large costs of initial clearing, continuous maintenance, and patrolling, trails can quickly achieve energetic profitability under a wide variety of parameter values. An example representative of field conditions is shown in Fig. 2 (50-m trail with unladen workers comprising 42% of traffic; $u = 0.42$, the average value from the studies cited in Appendix A, Table 3), of which half are assumed to be standby clearers ($u_S = 0.5$). At the typical foraging rate reported by Bruce and Burd (2012), clearing a 50-m trail would become profitable from 0.5 days of use onwards. That is, in less than a single day, the energetic savings from foraging on a cleared trail would have amortized the cumulative costs of clearing. Note that the cost incurred by the standby workforce, although modest, is many times larger than the cost for the actual removal of obstructions (Fig. 2).

Effect of trail length on trail profitability

With otherwise fixed conditions ($u = 0.42$, $u_S = 0.5$), trail length affects a colony's energetic benefit in a counterintuitive way: the benefit of trail clearing B is proportionally higher on longer trails (see Fig. 3). As a result, longer trails achieve profitability earlier than short ones (also see Fig. 5). This relationship follows from the superlinear scaling of forager numbers with trail length (Bruce and Burd 2012), which we incorporate in the model (see Appendix A, Equation 4). Given the scaling relationship, the pattern in Fig. 3 reflects the intuitive idea that the benefit of a cleared trail depends on how much it is used.

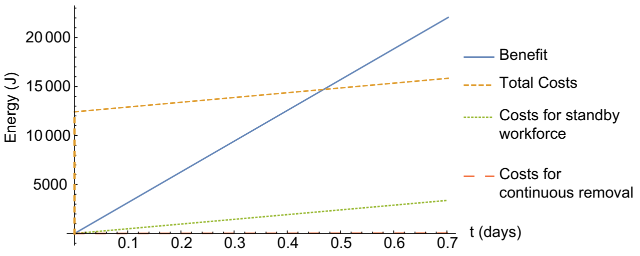


Fig. 2 Cumulative energetic foraging expenditure over time. Trail length = 50 m, percentage of unladen workers $u = 0.42$, and standby workers as fraction of all unladen workers $u_S = 0.5$. After the break-even point at 0.5 days of use, the cumulative benefit of foraging on a cleared trail is larger than the cumulative costs of trail clearing. The offset of total costs at $t = 0$ represents the initial clearing cost

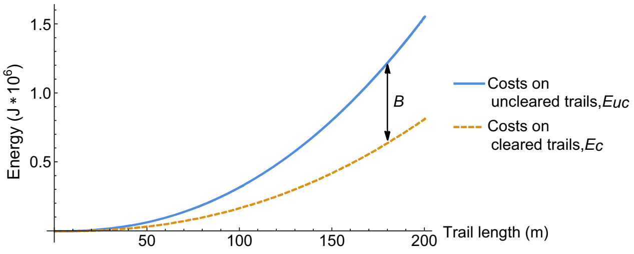


Fig. 3 Scaling of daily energetic expenditure with trail length, on cleared and on uncleared trails, assuming u = 0.42 and u_S = 0.5. The energetic benefit of trail clearing B (i.e., the difference between foraging costs on cleared and uncleared trails, E_C and E_{UC}) increases with trail length

Effect of standby workforce proportion on trail profitability

Because the proportion u_S of standby trail clearers among the unladen workers in the traffic stream is unknown, we determined the ranges for u and u_S under which trail clearing can be profitable (i.e., a break-even point is reached in a finite time). We considered a lower boundary for u at 13.1% and an upper boundary at 80%, the range of unladen workers observed in field colonies (Appendix A, Table 3). Except at the highest values of u and u_S, trail clearing can be profitable (Fig. 4). At the maximum observed fraction of unladen workers, $u = 0.8$, a cleared 50 m trail can remain profitable with a standby workforce of up to $u_S \approx 0.3$. Even if all unladen workers are standby clearers (i.e., $u_S = 1$), such a trail would remain profitable if a fraction up to u = 0.54 of workers in the traffic stream were unladen. Only for values of u between 0.54 and 0.8 does the fraction u_S need to be lower than unity for trails to remain profitable (Fig. 4).

The duration of trail usage needed for clearing to be an energetically profitable option depends nonlinearly on the size of the standby workforce, especially near the boundaries of profitability. Profitability landscapes for u_S = 1 and 0.3 are shown in Fig. 5. For most trail lengths and proportions of unladen workers, cleared trails reach energetic profitability in less than a day of use. At the boundary of unprofitability, however, the break-even times rapidly increase to weeks, months, and even years. The point at which this occurs depends only on the proportion of unladen workers u and standby workers u_S but is independent of trail length. Under plausible but relatively narrow ranges of parameter values, then, it is possible for trail clearing to require long payback times.

Effect of speed gain on cleared trails

Our measurements showed that ants move about half as fast as on uncleared trails as on cleared trails (i.e., speed coefficient for laden ants on uncleared trails w_L = 0.44 and for unladen ants w_{UL} = 0.5; see Appendix A, Table 2). If we assume a lesser disadvantage on uncleared trails (i.e., a higher value of w), the conditions under which trail clearing is profitable are narrower. In particular, the maximum sustainable proportion of unladen workers (as shown in Fig. 4) decreases (see Fig. 6). In line with this, break-even times increase (e.g., from 0.5 to 4.1 days for $w = w_L = w_{UL} = 0.7$, on the previous example trail of $l = 50$ m, $u = 0.42$, $u_S = 0.5$). Thus, the obstructing effect of an uncleared trail and the potential speed gain on a cleared surface is a deciding factor on whether trail clearing can be profitable and on how long it takes to reach profitability.

Discussion

We have presented a comprehensive model of the energetic balance of trail clearing in leaf-cutting ants. Our model allows us to calculate the conditions under which trail clearing can be energetically profitable, and how long it takes before trails reach profitability. Previous work by Howard (2001) had suggested that the volume of foraging traffic carried by a cleared trail would easily make trail clearing energetically favorable.

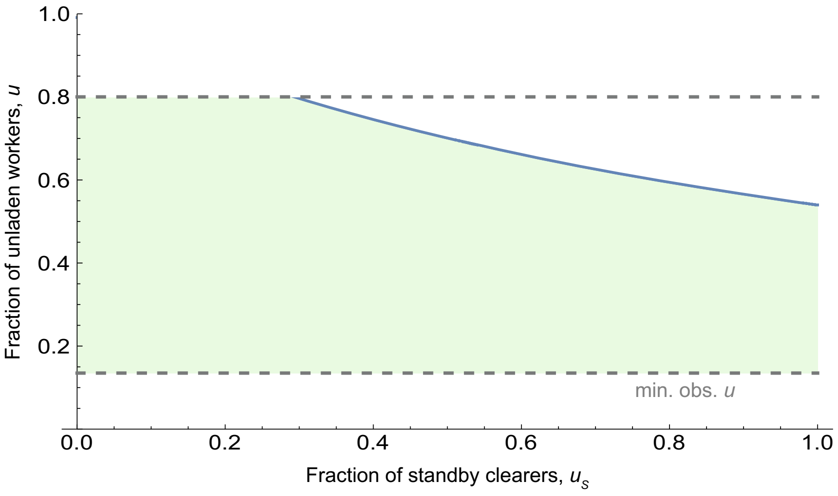


Fig. 4 Maximum sustainable proportion of unladen workers u for any standby workforce size u_S (given as fraction of u) on a 50-m trail. *Dashed lines* indicate range of observed proportions of u in the field. The intersection of this range and the area under the curve gives the expected conditions under which we expect to find profitable trails. Under most observed values for u, trails remain profitable even if the entire unladen workforce act as standby clearers (i.e., $u_S = 1$) and incur costs accordingly

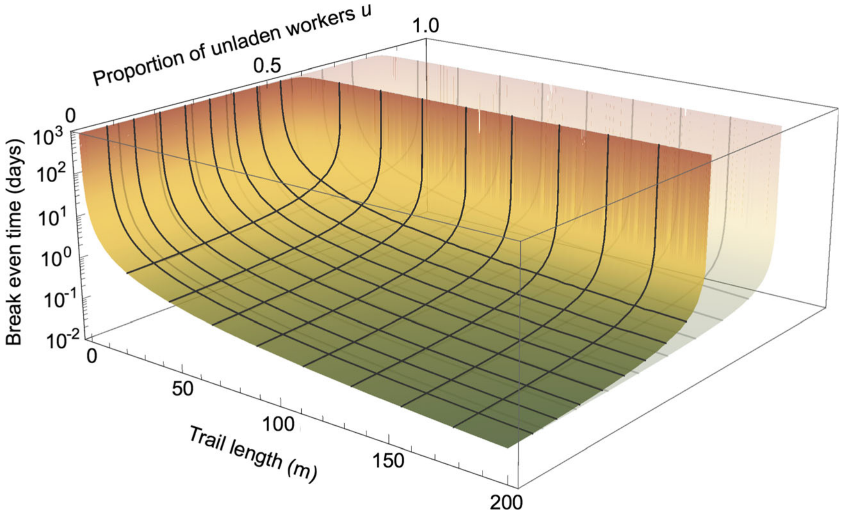


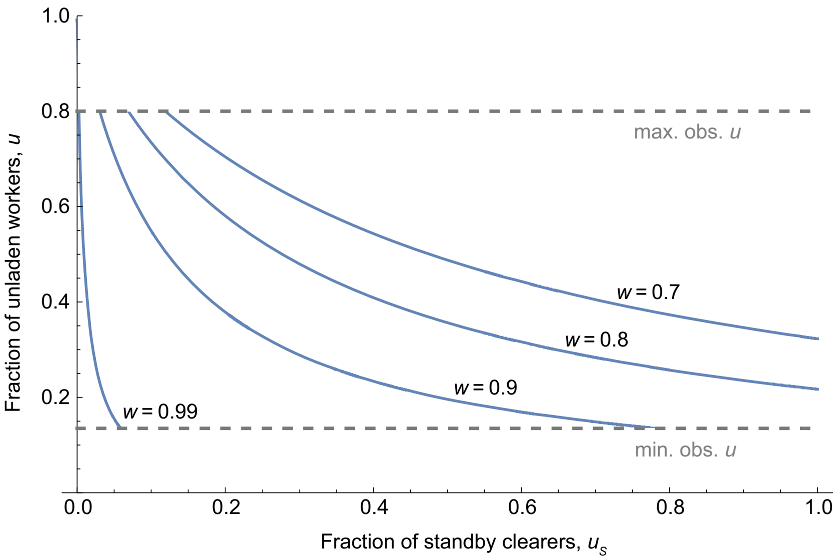
Fig. 5 Energetic break-even times as a function of both trail length and percentage of unladen workers in the traffic flow, u. The solid surface shows results for the assumption that all unladen ants are standby clearing ants ($u_S = 1$), while the transparent surface corresponds to $u_S = 0.3$, implying that most unladen ants perform tasks other than clearing. The graph shows that trail clearing achieves rapid break-even times for most combinations of trail length and unladen worker fraction. However, the time to reach a break-even point rises sharply to months and years, when the proportion of unladen workers is high or trails are short

Our model largely confirms this idea: in many scenarios, the time to energetic break-even can be very short. Nonetheless, a full exploration of the parameter space shows that under an array of realistic circumstances, the maintenance of a cleared trail can be very expensive. In such scenarios, cleared trails may only amortize after months or years—or may even never be profitable at all.

Profitability depends on a number of factors, including the number of standby clearers a colony needs to deploy on its trails for maintenance. If the proportion of unladen ants in the traffic flow is high, trail clearing can be profitable only if the standby workers make up a small fraction of the unladen total (Fig. 4). If the standby clearers comprise too large a fraction, trail clearing can be energetically unprofitable. Furthermore, as the speed advantage provided by a cleared trail surface diminishes, the tolerable fraction of standby clearing ants declines (Fig. 6). Thus, the speed gain on cleared trails has a strong influence on trail profitability. If it is not high enough, trail clearing may never pay off, no matter how much the cleared trail is used. This suggests that it would be advantageous for *Atta* colonies to possess a regulatory mechanism for clearing behavior that takes speed gain into account. Such a mechanism might involve direct assessment of trail conditions on speed or use indirect cues of the expected average speed in relation to trail conditions.

Our calculations of energetic benefits of trail clearing are conservative and represent a lower bound: in addition to our modeled assumptions, traveling over leaf litter obstruction

Fig. 6 Influence of different values for expected speed gain w on clearing profitability (cf. Fig. 4). As the expected speed gain is reduced (e.g., as $w = w_L = w_{UL}$ approaches 1), the range of conditions for profitable trail clearing (as given by the intersection of area under the curve and the observed range of unladen workers u) decreases superlinearly. *Dashed lines* indicate minimum and maximum observed values of u



might be proportionally costlier for laden workers, and reduced net energetic expenditures of foraging on cleared trails might lead to larger fragments being cut. While our approach focuses on the benefit derived by foraging workers, unladen workers not involved in trail clearing may also benefit from using cleared trails. Our model compares cleared and uncleared trails assuming equivalent amounts of leaf harvesting. However, faster movement on cleared trails increases the potential number of round-trips per forager, and trail clearing might therefore increase the potential resource intake during a foraging day.

Atta colonies opportunistically exploit fallen branches, rocks, or other naturally exposed features as part of their trail networks. While these trail segments might introduce slight detours from the direct path to the harvest site, they also require no clearing or maintenance and offer a movement speed benefit (Freeman and Chaves-Campos 2016). Howard's (2001) calculation of clearing costs accounted for such features as 9.3% of the total trail length. Farji-Brener et al. (2007) found that naturally exposed branches made up 30% of the length of *A. cephalotes* trails in Costa Rica. For simplicity, we have used Howard's (2001) estimates with their implied proportion of 9.3%, but other values could be modeled by simple adjustment of the clearing cost per unit of trail length.

The genus *Atta* occurs in diverse environments including both rainforests and grassland. Our qualitative predictions should be largely transferable to other rainforest-living *Atta* species: parameters used in our model (i.e., rate of leaf litter fall, effect of leaf litter on movement speed, achievable speed gain) would be similar among tropical lowland forests. Quantitative differences (e.g., in the rate of leaf-fall or in the impact of morphological differences on the movement speed) could, however, be effortlessly integrated into the model.

For grassland *Atta* species, litter fall on trail surfaces is likely to be reduced, so that trails need less maintenance. If, as a result, a smaller reserve of potential trail clearers is needed on trails, then the cost of trail clearance is lowered. The advantage of cleared trails would remain nearly unchanged: laden workers of the grassland species *Atta laevigata* moved 2.4 times faster on cleared than on uncleared trails (4.1 vs. 1.7 cm/s, respectively) (Bouchebti 2015), similar to the advantage we found for forest species of *Atta* (1.37 vs. 3.14 cm/s, respectively—see Appendix A, Table 3). With lowered maintenance cost and similar locomotion benefits, we expect that foraging trails would be cleared more readily and be more prevalent among grassland than among forest species.

Other than *Atta*, the ant genera *Formica*, *Lasius*, *Pogonomyrmex* (Hölldobler and Wilson 1990), *Messor* (Acosta et al. 1993; Plowes et al. 2013), *Camponotus* (Marlin 1971), *Iridomyrmex* (Greaves and Hughes 1974), and *Acromyrmex* (Gamboa 1975; Wetterer 1995) are known to likewise construct cleared trails. Our approach is applicable for those genera as well but will require a detailed investigation of the costs of trail construction and the speed-based benefit they each derive. Extrapolated, our model can serve as a template for other infrastructure constructing social insects, e.g., tunneling ants or termites. However, assessing the benefit they receive from constructing tunnels will likely be more complex than the speed-based benefit in *Atta* and involve predator avoidance and protection from environmental conditions.

Literature on *Atta* trails overwhelmingly focuses on cleared trails. However, uncleared trails do exist in the field: we have observed such trails persisting for weeks. This may reflect a delayed onset of clearing or indicate that the conditions on this trail do not allow for trail clearing to be profitable. It would be interesting for future research to investigate whether there is any correlation between actual trail clearance in the field and the predicted profitability of clearing it.

Based on the model results, we make qualitative predictions about the behavior we expect to find in the field and suggest experimental approaches for their investigation:

The proportion of unladen workers on trails should coincide with the intensity of leaf litter fall. In environments where the rate of leaf fall is low (e.g., in grassland), we expect to find fewer unladen workers than in forest habitats. *Atta* colonies have been shown to be sensitive to litter fall in their trail design: Farji-Brener et al. (2014) found that the branching angles of newly constructed paths from trunk trails to harvesting sites differed between forest and grassland environments. The resulting geometry minimized maintenance costs in the forest where long-term maintenance costs were high but minimized travel times in grassland areas with high sun exposure and increased desiccation risk but little litter fall. Likewise, we expect that within the same colony, trails receiving higher leaf fall should show more unladen workers. A detailed investigation of unladen worker numbers under these conditions, as well as potential differences in their behavior, could offer indications as to the validity of our assumptions.

We further predict that trails should remain uncleared if the duration of resource exploitation will be shorter than the break-even time. Such short exploitation times are conceivable for scattered or ephemeral resources, e.g., fallen flowers or ripe fallen fruit, resources that would decompose rapidly in a tropical rainforest. Previous research on *Atta* foraging has focused almost exclusively on their use of cleared trails, but we have observed foragers collecting fallen *Guapira standleyana* fruit on uncleared trails (manuscript in preparation). Offering resources that in nature would be ephemeral near established trails—and observing trail clearing to these—would be a possible method to investigate this prediction.

Likewise, we expect the quality of the foraged resource to correlate with the trail clearing intensity: a low-quality resource will provide comparably less energy to the colony, while the cost of trail clearing will be identical. Controlled offering of different resources—and the observation of time of onset and intensity of trail clearance—would provide insight into the influence of resource quality.

Shepherd (1982) also inferred that trail construction would be most beneficial for colonies exploiting high-quality, long-lasting resources. Likewise, we agree with his assumption that larger colonies should more frequently clear trails. However, our reasoning on this point is based on the observed superlinear scaling of forager numbers with trail length (Bruce and Burd 2012) and the corresponding higher relative resource intake on longer trails. An investigation into trail clearing occurrence in colonies of different sizes could investigate this hypothesis.

The extended use of uncleared trails by leaf-cutting ants has not been the focus of research and is poorly described. Research on uncleared trails, the duration of their use, the conditions under which they occur, and the functional role of unladen workers might shine further light on trail clearing profitability and deserve further study.

Acknowledgements The authors would like to thank the Smithsonian Tropical Research Institute and its staff in Panama for providing research facilities, as well as the Neurobiology and Behavior workgroup at the University of Konstanz, Germany and its members for many stimulating discussions.

We are further grateful for the valuable input of two anonymous reviewers which helped us improve the quality of the submission.

Compliance with ethical standards

Funding TB was supported by Monash University postgraduate scholarships and by CSIRO Data61. Model development and field work were partially supported by Australian Research Council grants A19800465 (to MB) and DP110101413 (to BM).

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