Leaf caching in the leafcutting ant *Atta colombica*: organizational shift, task partitioning and making the best of a bad job

ADAM G. HART & FRANCIS L. W. RATNIEKS

Department of Animal and Plant Sciences, University of Sheffield

Leafcutting ants (*Atta* and *Acromyrmex*) sometimes form piles or caches of leaves on foraging trails. Laboratory experiments have shown that leaf caching at the nest entrance by *Atta cephalotes* and *Atta colombica* is adaptive because it occurs when a colony's leaf delivery rate exceeds its leaf-processing rate and serves to increase the probability that a dropped leaf is eventually recovered. We examined the occurrence and adaptive value of leaf caching on foraging trails in field colonies of *A. colombica* in Panama. The probability of leaf caching was positively related to trail traffic with cache locations being frequently associated with changes in gradient or terrain along the trail. Artificially blocking foraging trails resulted in caching behaviour but only when the blockage was near the leaf source or the nest entrance. This mirrors individual leaf dropping on trails and bottleneck-induced nest entrance caching in the laboratory. Leaves were recovered more rapidly from caches but because leaves were not selected according to forager size they were transported back to the nest more slowly than normally foraged leaves. Thus, whilst caching provides benefits, by increasing the likelihood of leaf recovery, it imposes a cost through mismatching forager and load size. Leaf caching is an example of an organizational shift (from direct foraging to foraging with task partitioning) and we provide a minimum estimate of the cost of this shift. Leaf caching encompasses two behaviours, leaf dropping and cache formation. Leaf dropping, and therefore the switch to task partitioning, is not in itself adaptive and cache formation has costs as well as benefits. We propose that leaf caching is making the best of a bad job if for some reason it is necessary for foragers to put down their leaf.

© 2001 The Association for the Study of Animal Behaviour

Insect societies have several mechanisms for adaptively adjusting their work organization to both internal and environmental variation (Gordon 1996). The sizes of the workers themselves can change. For example, colonies in the process of being established by a lone queen frequently rear only nanitic (small) workers, and species in which large, major, workers are reared frequently do so only when the colony has reached a large size (e.g. *Solenopsis invicta*: Oster & Wilson 1978; Tschinkel 1988). The tasks that the workers do are also extremely flexible. For example, a colony of honeybees, *Apis mellifera*, can rapidly adjust the numbers of foragers and receivers involved in nectar collection and storage (Seeley 1995; Anderson & Ratnieks 1999). Similar changes in division of labour occur in practically all species, and are characterized by workers performing one or a subset of tasks for a relatively long period (days or more; Oster & Wilson 1978; Robinson 1992; Seeley 1995). Another way that work allocation can change is by task switching, in which

Correspondence: A. G. Hart, Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K. (email: bop98agh@sheffield.ac.uk).

a worker capable of performing several tasks allocates more of her time to one of them (Gordon 1989). But work organization can also be changed by changing the structure of the work itself. For example, a task that is normally performed by one worker can be divided into two subtasks (Ratnieks & Anderson 1999).

There are several examples of this change in the structure of work. In *Vespula* wasps, nectar foragers transfer their load to receivers only in large colonies (Akre et al. 1976). In leafcutter ants (*Atta*) there are a variety of different ways in which the leaves are cut up and brought back to the nest (Hart & Ratnieks 2000 and references therein). One highly flexible change in work organization in *Atta* concerns leaf collection by foragers. Normally, a leaf piece is carried back to the nest by one worker, but the task can be partitioned, with either direct leaf transfer between foragers or indirect transfer with the formation of a cache somewhere along the trail. For example, *A. cephalotes* foragers sometimes use a two-stage relay process involving direct leaf transfer between foragers where trunk and side trails join (Hubbell et al. 1980). Indirect transfer via caches has been seen in a wide range

227

Table 1. The incidence of caches on two trails of each of five colonies

Trail number (colony.trail)	Trail length (m)	Cache position	Distance from entrance (m)	Number of discrete caches
1.1	45	Intersection of foraging trail and hiking trail	35	3
		Base of 25° slope	20	1
1.2	60	Intersection of foraging trail and hiking trail	10	1
2.1	65	In manmade concrete drainage flume	40	2
2.2	85	No caches		0
3.1	80	Base of 45° slope	15	1
		Intersection of foraging trail and hiking trail	55	2
3.2	45	Bare earth, level ground	30	2
			40	3
4.1	75	Intersection of foraging trail and hiking trail	35	2
4.2	45	Bare earth, level ground	35	2
			20	1
5.1, 5.2	60, 85	No caches		0

of trail locations from leaf source to nest entrance, for example at trail junctions and by obstacles (reported in Hart & Ratnieks 2000).

Hart & Ratnieks (2000) suggested that nest entrance caches in *A. colombica* and *A. cephalotes* are an adaptive, flexible response to bottlenecks arising when forage input exceeds leaf-processing rate. Laboratory experiments showed that discrete piles of leaves at the nest entrance grow through positive feedback and that cached leaves have a higher probability of being recovered than scattered leaves. Therefore, caching can reduce leaf losses arising from an imbalance between foraging and processing rates. However, leaf caches also occur along foraging trails (U. G. Mueller, personal communication), which are commonly over 100 m long (Hölldobler & Wilson 1990). These can be properly studied only in the field.

We investigated the occurrence and adaptive importance of leaf caching in field colonies of *A. colombica.* Through a combination of observation and experiment we set out to investigate: (1) the natural occurrence of leaf caches on trails and how trail traffic and topography influence the switch to partitioned foraging; (2) the influence of trail position on cache formation at artificial blockages; (3) levels of leaf dropping (i.e. inefficiency) on trails during normal foraging; (4) whether caching leaves increases the probability of leaf recovery in comparison to laboratory results; and (5) the efficiency of leaf recovery from caches, by comparing the relationship between forager weight, leaf load weight and forager speed for foragers foraging normally and from a cache. Our results allowed us to determine some of the conditions under which foraging switches from single worker transport to cache-mediated task partitioning and to estimate the cost of this organizational flexibility.

METHODS

Study Site and Species

We studied 17 colonies of *A. colombica* in Gamboa, Panama during March–June 2000. All colonies were more than 3 years old (based on local sources) and had at least three foraging entrances with well-defined foraging trails. Traffic on all trails was greater than 15 foragers carrying leaves/min.

Cache Occurrence and Relationship to Trail Traffic

We selected colonies 1–5 to study the normal occurrence of caches. We randomly chose two foraging trails per colony and flagged them at 5-m intervals. Table 1 gives the trail lengths (excluding the trail up the source tree). We patrolled the trails at ca. 1000 and 1800 hours for 11 days. A cache was defined as any accumulation of leaves greater than five fragments in a square of 20×20 cm. We recorded cache size and position. To give an estimate of trail traffic we counted for 60 s the number of foragers carrying leaves past a fixed point for each trail of each colony at each patrol.

Cache Occurrence and Relationship to Distance Along Trail

Foragers in laboratory colonies can be induced to cache leaves at the nest entrance by artificially blocking the entrance (Hart & Ratnieks 2000). Preliminary observation suggested that foragers on trails could also be induced to cache by blocking the trail. We used colonies 1–5 to investigate the effect that the position of an artificial trail blockage, relative to either leaf source or nest entrance or both, had on the probability of cache formation. We randomly chose one trail from each colony and flagged it at 5-m intervals from the foraging entrance to the leaf source to provide known blockage points. All colonies were foraging from trees and the leaf source was taken as the tree base. At each 5-m point along the trail we counted the number of laden foragers passing the point for five 1-min periods at 5-min intervals. We then placed a soil-filled canvas bag ($100 \times 100 \times 25$ cm) on the trail at the blockage point such that the trail and at least 25 cm of ground surrounding the trail on either side were

obstructed. We recorded the blockage on video for the duration of the experiment to quantify trail traffic on the source side of the blockage. The number of leaves dropped at the source side of the blockage was counted at 5-min intervals for 20 min. Accumulations of fewer than five dropped leaves were not counted as a cache and were ignored. We removed the blockage after 20 min. We did this three times at each 5-m point (with at least 1 h between trials) on each trail for all five colonies.

Natural Leaf Dropping on Trails

We used colonies 6–9 to investigate whether cache formation is related to normal leaf-dropping behaviour. We selected an approximately level trail from each colony at random, flagged it at 5-m intervals and cleared it of dropped leaves. We patrolled the trail every 10 min for 2 h and counted the number of leaves dropped in each 5-m trail section. Any dropped leaves were removed during each patrol. We counted the number of laden foragers passing the midpoint of each trail for 1 min every 30 min, giving five measurements.

Leaf Collection

Noncached sources

We also used colonies 6–9 to investigate leaf collection from noncached sources. We took leaf fragments from foragers and placed them on the trail individually near the source, at the midpoint and at the nest entrance. We counted the number of foragers passing within 1 cm of the leaf until it was picked up and moved further than 5 cm. We did this for 50 leaves at each point.

Cached sources

To investigate leaf collection from cached sources we laid out on the trail within a 10-cm square experimental caches of 50 leaves, taken randomly from foragers on the experimental trail. We counted foragers walking over the cache or otherwise touching it until 25 leaves had been removed from the cache. We did this five times at the source, midpoint and nest entrance for eight trails randomly selected from eight colonies (colonies 10–17).

Efficiency of Cache Collection

To test whether collection from caches is as efficient as normal foraging, we took 100 leaves from foragers and marked them with white typing correction fluid. They were placed midway between the nest entrance and the leaf source within a 10-cm square. We collected 50 marked leaves, and the foragers carrying them, from the nest entrance and weighed them using a Sartorius BP61 balance (0.1 mg). We also weighed a sample of 50 normal foragers and their unmarked leaf pieces. For this we used colonies 1–5. We observed 20 foragers from each colony carrying marked leaves from the cache to the nest entrance. Any leaf transfer to other foragers was noted. Finally, we timed 30 foragers from colony 1 carrying
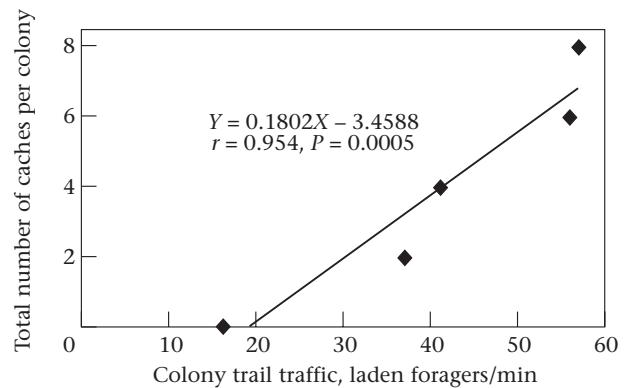
Figure 1. Relationship between the total number of caches observed and colony trail traffic.

marked leaves and 30 foragers carrying unmarked leaves over 50 cm of trail to obtain forager speeds.

RESULTS

Cache Occurrence and Relationship to Trail Traffic

We observed 20 caches. The total trail length across all colonies was 645 m (Table 1) which we patrolled 22 times giving an average of one cache per 709 trail-metres. Caches ranged in size from 18 leaves to 1000 ($\bar{X} \pm \text{SD}=213 \pm 273$: median $\pm$ IQR=90 $\pm$ 44, 250, N=20). They were observed in 11 different sites, with two sites having different caches on three occasions, five on two occasions and four on only one occasion. Twelve of the 20 caches (60%) were associated with clear topographical features. Eight caches (40%) formed at the intersection between a foraging trail and a human path, two (10%) at the base of steep slopes and two (10%) in a concrete drainage channel (Table 1). Eight caches (40%) formed on level ground with no obvious topographical features.

There was no difference between trail traffic on each of the two trails selected for each colony (*t* test: C1: t_{19}=0.10, P=0.92; C2: t_{19}=0.12, P=0.91; C3: t_{19}=0.43, P=0.67; C4: t_{19}=0.40, P=0.69; C5: t_{19}=0.08, P=0.94). Trail traffic combined across each trail differed significantly between each colony but did not differ significantly between the morning and evening (ANOVA: colony effect: $F_{9,219}$=156.50, P<0.001; time effect: $F_{1,219}$=0.44, P=0.51; interaction: $F_{9,219}$=0.63, P=0.77). The total number of caches observed for each colony over the study period and the combined colony trail traffic mean (day and night, trail 1 and trail 2 combined for each colony) were used for the analysis. There was a strong correlation between the number of caches observed and trail traffic (Fig. 1). Caches were not observed in colony 5, which had the lowest trail traffic ($\bar{X} \pm \text{SD}=16.0 \pm 4.2$ laden foragers/min: median $\pm$ IQR=16.5 $\pm$ 13, 19.8, N=22). Eight caches were observed in colony 3, which had the highest trail traffic ($\bar{X} \pm \text{SD}=57.4 \pm 7.7$ laden foragers/min: median $\pm$ IQR=55 $\pm$ 53, 62, N=22).
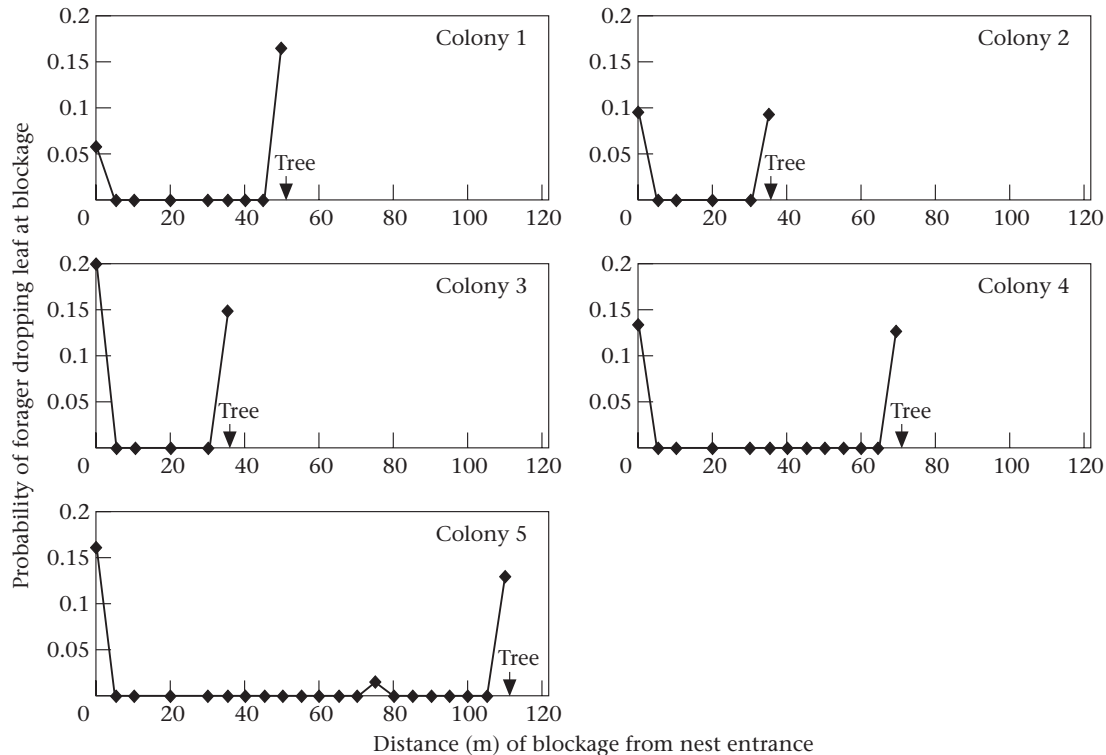
Figure 2. Probabilities of foragers dropping leaves at artificial trail blockages placed along the trail. Arrows represent the forage source tree.

Cache Occurrence and Relationship to Distance Along Trail

We calculated the probability of a forager dropping her leaf by dividing the number of leaves accumulated in each 5-min period of blockage by the number of foragers with leaves entering the blockage zone. There was a consistently strong effect of trail position on the probability of leaf dropping (Fig. 2). Between 6 and 20% of foragers dropped their leaves if the blockage was within 5 m of the nest entrance or the tree source. But if the blockage occurred elsewhere on the trail leaf dropping was zero, except for one trial in colony 5, when a cache developed 75 m from the nest entrance, 35 m from the leaf source.

Natural Leaf Dropping on Trails

Leaf dropping was greatest near the leaf source, diminishing roughly exponentially towards the nest entrance, without the rise at the entrance observed in leaf caching (Fig. 3). There was no apparent relationship between trail traffic and leaf dropping, although a sample size of four colonies weakens the power of detection.

Leaf Collection

Noncached sources

Trail lengths in the four colonies were 50 m except for C1, which was 60 m. Data were transformed (square root ($X+0.5$), Heath 1970). In all colonies there was no significant difference in the number of foragers that passed a

dropped leaf before it was recovered at the leaf source or the trail midpoint (t test: C1: $t_{98}= -0.73$, $P=0.47$; C2: $t_{98}=0.05$, $P=0.96$; C3: $t_{98}=1.45$, $P=0.15$; C4: $t_{98}=1.50$, $P=0.14$; Fig. 4). For each colony we combined source and trail midpoint data for comparison with nest entrance data. Significantly more foragers passed a dropped leaf at the entrance before it was recovered than at the source and trail midpoint in all colonies (t test: C1: $t_{148}=12.90$; C2: $t_{148}=16.40$; C3: $t_{148}=14.00$, C4: $t_{148}=13.10$; all $P<0.001$; Fig. 4). Combining data across colonies, a mean $\pm$ SD of 32.6 ± 16.6 ($N=200$) ants passed a leaf at the entrance before it was recovered, but only 4.7 ± 4.1 ($N=400$) for leaves at trail midpoint and leaf source.

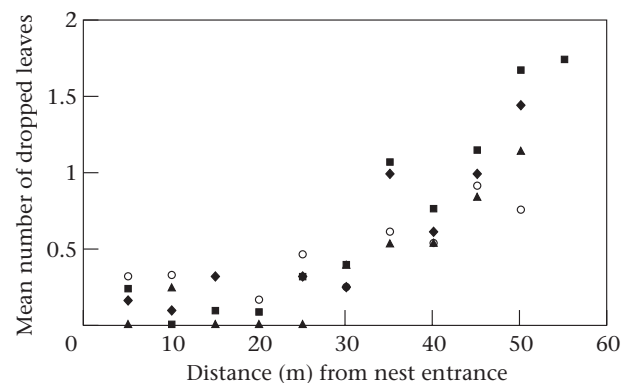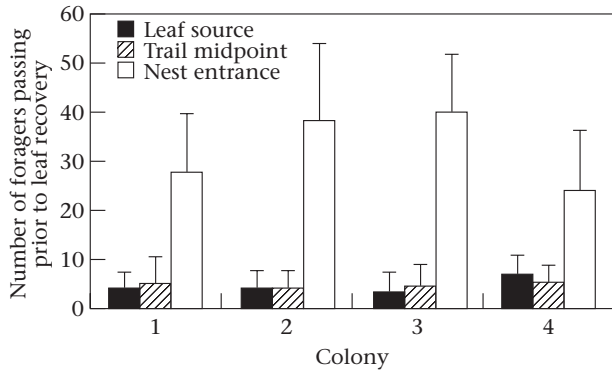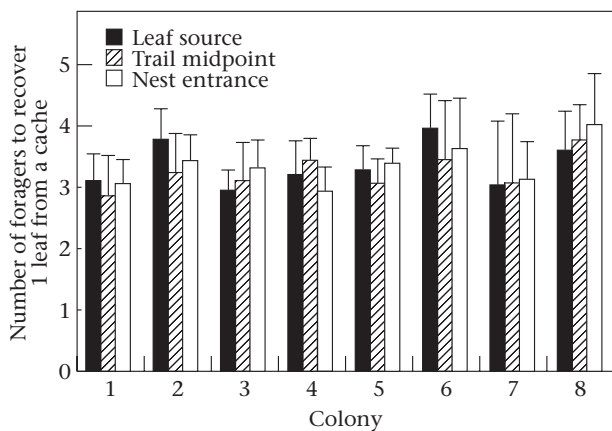**Figure 3.** Natural leaf dropping along foraging trails. Mean trail traffic/min$\pm$SD: ■: 51.8$\pm$6.5; ◆: 63.0$\pm$3.7; ▲: 42.8$\pm$3.3; ○: 68.0$\pm$4.5.

Figure 4. Recovery of a single leaf placed individually at three points along foraging trails for four colonies ($N=50$ leaves for each bar). Error bars indicate SD.

Figure 5. Recovery of a single leaf from a cache of 50 leaves at three points along foraging trails for eight colonies ($N=5$ trials for each bar). Error bars indicate SD.

Cached sources

Data were transformed (square root (X), Heath 1970). There was no significant effect of trail position on cache recovery for any colony (two-way ANOVA: $F_{2,96}=0.55$, $P=0.58$; Fig. 5). There was significant intercolony variation (two-way ANOVA: $F_{7,96}=3.32$, $P=0.003$) but no significant interaction between colony and trail position (two-way ANOVA: $F_{7,96}=0.52$, $P=0.92$). When we combined data across colonies and trail positions, we found that a mean $\pm$ SD of 3.36 ± 0.65 ($N=120$) foragers were needed to collect each leaf from a cache. This is significantly lower than the 4.7 foragers required to recover noncached leaves from the leaf source and trail midpoint combined (t test: $t_{518}=3.45$, $P=0.0006$) and the 32.6 foragers required at the nest entrance (t test: $t_{318}=19.3$, $P<0.0001$).

Efficiency of Cache Collection

The fresh weights of foragers were not significantly correlated with load weight for leaves recovered from a cache but were for leaves the foragers cut themselves (Fig. 6). The time taken for foragers under normal conditions to cover 50 cm of trail was significantly lower than the time taken by foragers recovering leaves from caches ($\bar{X} \pm SD=12.7 \pm 2.6$ s, $N=30$ versus $\bar{X} \pm SD=20.9 \pm 12.5$ s, $N=30$; two-sample, unequal variance t test: $t_{31}=3.49$, $P=0.0007$). Furthermore, no leaf transfers between foragers were observed ($N=20$ ants for each of four colonies).

DISCUSSION

Leaf caches occurred on trails, but not frequently. Overall, we found one cache for every 709 m of trail with an average of 213 leaves/cache. We never observed direct leaf transfer. Therefore, the majority of leaves were neither cached nor transferred but rather were carried directly to the nest by a single forager without task partitioning.

Leaf caching on trails was, however, strongly positively correlated with trail traffic, with caches only found on trails with trail traffic greater than 20–25 laden foragers/min. This suggests that a level of trail traffic exists below which caches cannot form. Thus, a transition occurs in *Atta* foraging, with caches forming through positive feedback only above this level of trail traffic. However, because 60% of caches were at certain topographical features, high trail traffic is not the only causal factor in cache formation. Forty per cent of caches occurred at points where human trails and ant trails intersected suggesting that disturbance plays an important causal role in caching. Changes in forager speed or ease of carriage, such as probably occur at the bases of steep slopes and where trails crossed a concrete drainage channel, may also be important (20% of caches).

We could induce caching by experimentally blocking trails. However, even though natural caches occurred at all positions along trails, we could induce it only at the nest entrance or near the leaf source. Our failure to induce caching at other sites was probably due to our single blocking method being less effective than some of the natural disturbances that induced caches. Leaf caches at the nest entrance occur frequently in natural colonies (A. G. Hart, personal observation) and can be readily observed in the laboratory at times when the leaf processing rate drops below the foraging rate (Hart & Ratnieks 2000). Caching has been hypothesized to detoxify leaves (Vasconcelos & Cherrett 1996) but this can be ruled out here because leaves from the same tree normally entered the nest without any caching. Piles of leaves are often found in chambers just inside the nest entrance (A. G. Hart, personal observations). It may be that near the nest entrance foragers drop their leaves when they can no longer proceed (as would occur naturally inside the nest) and that blocking the trail near the entrance triggers this behaviour. That this occurs only very near the nest entrance, both in the field and in the laboratory, suggests that positional information is available to foragers. Other studies provide further evidence for this idea. For example, leafcutting ants are less aggressive further from the nest (Jutsum 1979) and soil from around the nest entrance is attractive to *Pogonomyrmex badius* workers (Hangartner et al. 1970).

Near the leaf source it may be more efficient for foragers encountering a blockage to drop their leaf and return to
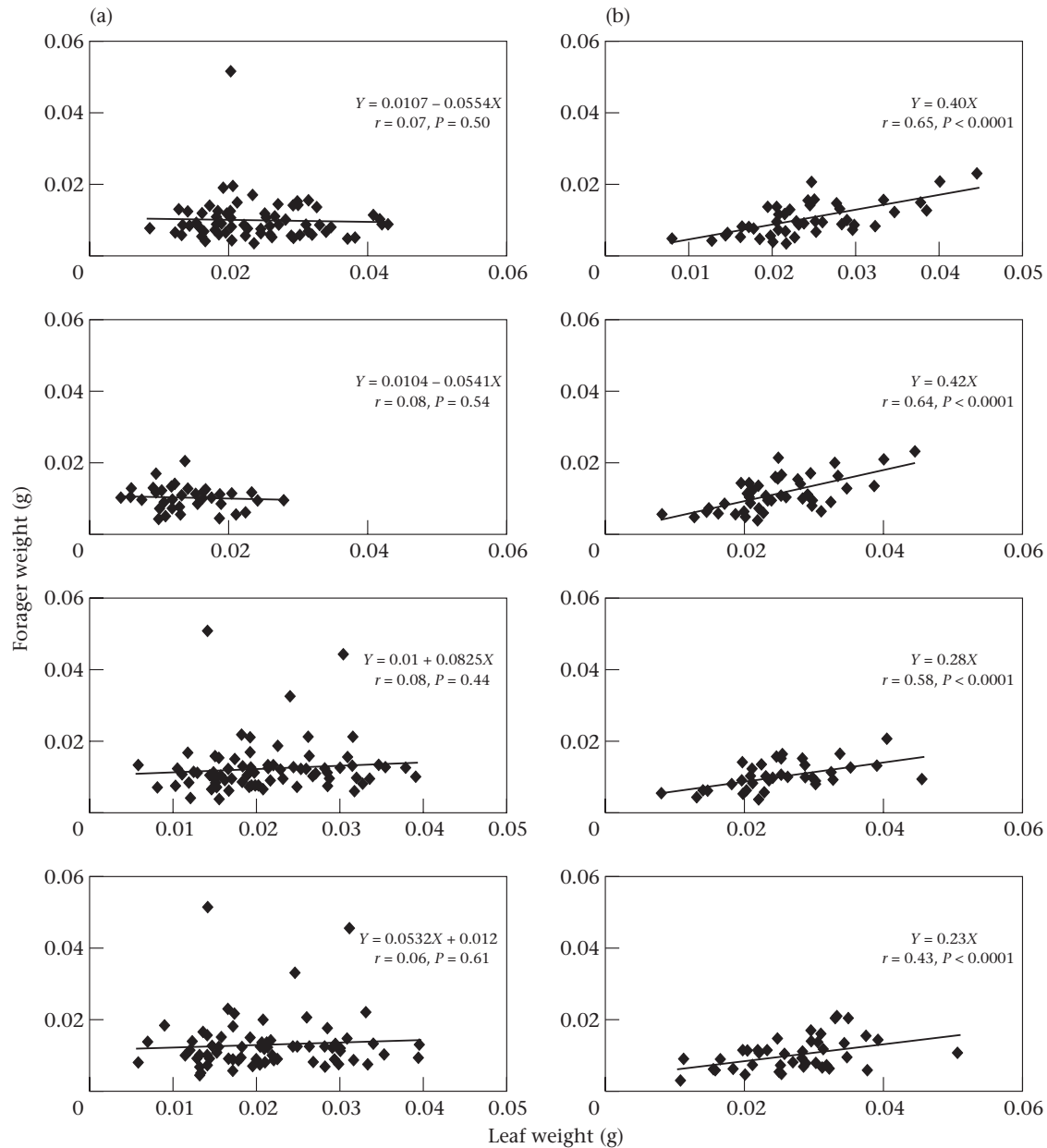
Figure 6. Relationship between forager fresh weight and leaf load fresh weight for (a) foragers recovering cached leaves and (b) foragers carrying leaves they had cut themselves (N=50 in all cases).

the source rather than avoid or try to bypass the blockage, especially given the high likelihood that a dropped leaf will be retrieved by other ants (this study). However, it is puzzling that leaf caching at trail blockages occurred only within 5 m of the base of the source tree in all but one case. The leaf-dropping observations provide a more likely explanation. Under normal foraging conditions we found that the closer foragers were to the leaf source the more likely they were to drop their leaves. The trails selected for the observations were on level ground and so the only topographical transition was from the steep slope of the leaf source tree to the level ground of the trail. This topographical situation was closely linked with cache formation under normal foraging conditions. Therefore, we suggest that foragers cache leaves at

blockages near the source tree, and are more likely to drop leaves at this point even in the absence of blockages, because of the change in trail topography, that is from vertical tree trunk to horizontal ground.

Cached leaves were more likely to be recovered than noncached leaves at all points along all trails. This was especially the case near the nest entrance, where cached leaves were nearly 10 times more likely to be recovered per ant than noncached leaves. This provides very strong field evidence to support Hart & Ratnieks's (2000) a priori hypothesis that caching has the benefit of increasing the probability of recovery of dropped leaves. Caches may act to attract foragers more strongly than scattered leaves or provide more stimulus to pick up leaves.

As found in many studies, there was a positive correlation between forager weight and size of leaf carried (e.g. Wetterer 1990, 1994; Vanbreda & Stradling 1994). But we also found that when recovering cached leaves foragers did not select leaves based on their size. Furthermore, by sampling foragers and leaves at the nest entrance we allowed for any leaf transfer between foragers, which occurs in *Acromyrmex* (A. G. Hart, personal observation) and *A. cephalotes* (Hubbell et al. 1980). In any case, we did not observe any leaf transfers when following individual foragers. A mismatch of foragers and leaf pieces led to foragers carrying previously cached leaves more slowly than those they cut themselves. Laden foragers travelled at a fairly uniform speed over the trail, shown by the variation in times taken to cover 50 cm by normal foragers ($\bar{X} \pm SD = 12.7 \pm 2.6$ s). Therefore, large ants carrying small leaves from caches probably travel at the uniform trail speed whereas small ants carrying large leaves go more slowly as shown by the variation in times of cache recovery foragers ($\bar{X} \pm SD = 20.9 \pm 12.5$ s). The tendency of leafcutting ants to recover leaves from caches and the effect that load selection has on trail speeds makes this an ideal system to investigate and manipulate traffic flow on ant trails. Overall, the recovery of leaves from caches is inefficient because of reduced forager speed. This allows us to quantify, for the first time, the cost of the organizational shift between normal foraging and task partitioning. It takes 70% longer to transport leaves back to the nest from a cache than without caching. This cost is an underestimate because it does not include time wasted in dropping and recovering the leaf (Hart & Ratnieks 2000) and the cost of occasional nonrecovery.

Task partitioning has a high cost in leafcutting ant foraging. What possible benefit does it have? Caching may act to maintain in-nest processing of leaves at a high rate in the face of mismatched foraging and processing capacities. Ideally the forage delivery rate should be perfectly matched to the leaf-processing capacity, but even if mean delivery rate and mean processing capacity are matched then variance around the means will result in at least occasional periods when laden foragers are backed up. Reducing the number of foragers is one solution but it will result in a lowered overall harvest of leaves. Alternatively, the colony could produce more minor workers and dig more chambers to increase the leaf-processing capacity. But, except for periods of highest delivery, these additional workers will usually be idle. Leaf caching would provide a flexible buffer of leaves from which the colony can draw when delivery rates fall or processing capacity increases. However, it seems likely that this is not the case. If caching were a buffering response to mismatched capacities of in-nest processors and forage input then why did so many caches form at trail transition points? Similarly, the buffer hypothesis does not explain why there is such a pronounced tendency to form caches near the leaf source, where information on nest-processing rates is unlikely to be present. The nest entrance would be the most likely place for caches to form but none was observed there.

Possibly, the switch from normal foraging to caching is not in itself beneficial. Rather, it could be making the best of a bad job. It is important to differentiate between the two components of leaf-caching behaviour, namely leaf dropping and the formation of discrete piles. Dropping leaves is certainly not adaptive but there was a low level of accidental leaf dropping. Furthermore, it was more likely to occur at certain regions of the trail, principally near the source and at transition and disturbance points. Once leaves are being dropped, the adaptive value of the second component of caching behaviour, formation of discrete piles, becomes important. Foragers that for whatever reason have high tendencies to drop a leaf, can, by forming discrete piles of leaves at dropping zones, increase the likelihood that dropped leaves will be recovered. Thus, the cost of a mistake (the potential loss of a leaf fragment into which cutting and transporting effort have been invested) can be reduced through the benefit of caching.

References

Akre, R. D., Garnett, W. B., MacDonald, J. F., Greene, A. & Landolt, P. 1976. Behaviour and colony development of *Vespula pensylvanica* and *V. atropilosa* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society*, **49**, 63–84.

Anderson, C. & Ratnieks, F. L. W. 1999. Worker allocation in insect societies: coordination of nectar foragers and nectar receivers in the honey bee. *Behavioral Ecology and Sociobiology*, **46**, 73–81.

Gordon, D. M. 1989. Dynamics of task switching in harvester ants. *Animal Behaviour*, **38**, 194–204.

Gordon, D. M. 1996. The organization of work in social insect colonies. *Nature*, **380**, 121–124.

Hangartner, W., Reichson, J. M. & Wilson, E. O. 1970. Orientation to nest material by the ant, *Pogonomyrmex badius* (Latreille). *Animal Behaviour*, **18**, 331–334.

Hart, A. G. & Ratnieks, F. L. W. 2000. Leaf caching in leafcutting ants *Atta*: discrete cache formation through positive feedback. *Animal Behaviour*, **59**, 587–591.

Heath, O. V. S. 1970. *Investigation by Experiment*. London: Arnold.

Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: The Belknap Press, Harvard University Press.

Hubbell, S. P., Johnson, L. K., Stanislav, E., Wilson, B. & Fowler, H. 1980. Foraging by bucket brigade in leaf-cutter ants. *Biotropica*, **12**, 210–213.

Jutsum, A. R. 1979. Interspecific aggression in leaf-cutting ants. *Animal Behaviour*, **27**, 833–838.

Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects*. Princeton, New Jersey: Princeton University Press.

Ratnieks, F. L. W. & Anderson, C. 1999. Task partitioning in insect societies. *Insectes Sociaux*, **46**, 95–108.

Robinson, G. E. 1992. Regulation of division of labor in insect societies. *Annual Review of Entomology*, **37**, 637–665.

Seeley, T. D. 1995. *The Wisdom of the Hive*. Cambridge, Massachusetts: Harvard University Press.

Tschinkel, W. R. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant *Solenopsis invicta. Behavioral Ecology and Sociobiology*, **22**, 103–115.

Vanbreda, J. M. & Stradling, D. J. 1994. Mechanisms affecting load size determination in *Atta cephalotes* L (Hymenoptera, Formicidae). *Insectes Sociaux*, **41**, 423–434.

Vasconcelos, J. L. & Cherrett, J. M. 1996. The effect of wilting on the selection of leaves by the leaf-cutting ant *Atta laevigata. Entomologia Experimentalis et Applicata*, **78**, 215–220.

Wetterer, J. K. 1990. Load size determination in the leaf-cutting ant *Atta cephalotes. Behavioral Ecology*, **1**, 95–101.

Wetterer, J. K. 1994. Forager polymorphism, size-matching, and load delivery in the leaf-cutting ant, *Atta cephalotes. Ecological Entomology*, **19**, 57–64.