



Leaf caching in *Atta* leafcutting ants: discrete cache formation through positive feedback

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We examined the occurrence, mechanism and costs and benefits of leaf caching in laboratory colonies of two species of leafcutting ants, *Atta cephalotes* and *A. colombica*. If foragers returning to the nest are unable to enter because of a temporary bottleneck caused by leaves building up they may deposit their leaf pieces outside the nest entrance, forming a leaf cache. Similar leaf caches occur in the field at foraging trail junctions, obstacles on the trail and within nest entrance tunnels. Foraging ants carrying leaves were presented with different-sized leaf caches and the number dropping their leaves on the cache was recorded. The probability of a forager dropping her leaf was positively correlated with the size of the cache that she encountered. Therefore, positive feedback played a role in the formation of nest entrance caches. Cached pieces were more likely to be retrieved than noncached pieces but the time taken to retrieve leaf pieces from a cache was greater than from scattered groups of leaves. We suggest that the strategy of flexible nest entrance caching is an adaptive response to fluctuating food availability and collection.

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Insect societies face the challenge of coordinating a potentially massive workforce. This has led to the evolution of various strategies of work organization such as division of labour (e.g. Oster & Wilson 1978). Another less well-known strategy, task partitioning, is also important (Jeanne 1986; Ratnieks & Anderson 1999). Task partitioning describes situations where two or more workers contribute sequentially to a piece of work. Central to task partitioning is the concept of material transfer between workers, which may be achieved in two ways: either directly between two workers or indirectly via a cache.

Task partitioning occurs in foraging by leafcutting ants. These ants cut leaf pieces which are processed and used to grow a nutritive symbiotic fungus (Weber 1972). In *Atta cephalotes*, foragers may use a two-stage relay process involving direct transfer of leaf pieces from primary 'cutters' to secondary 'carriers' at junctions between side and main foraging trails. Alternatively, leaves may be transferred indirectly via caches at these sites (Hubbell et al. 1980; see Ratnieks & Anderson 1999 for a review of transfer). In *A. sexdens*, workers foraging in the canopy drop leaves to the ground where workers can collect them and transport them back to the nest (Fowler & Robinson 1979). These examples are all of transfer occurring close to the leaf source. Observations of field colonies suggest that leaf caching may occur in numerous locations along

the foraging trail, and within the nest. Leaf caches have been seen at trail junctions (Hubbell et al. 1980), by obstacles and during rainfall (U. G. Mueller, personal communication). Furthermore, excavations of nest entrance tunnels have uncovered accumulations of leaves in both *Acromyrmex* and *Atta* (A. N. M. Bot, personal communication). *Atta sexdens* nests have chambers of unknown function about 80 cm into the nest from foraging trails, which have been suggested to house soldiers but could equally act as leaf-caching sites (Jacoby 1952). Collectively, published and unpublished data suggest that leaf caching occurs regularly under field conditions and in a wide range of locations from source to nest.

Our observation of laboratory colonies of *Atta* suggested that caching occurred at the nest entrance when the leaf supply rate exceeded the colony's processing rate. When this occurs, foragers deposit pieces outside the nest entrance and discrete piles or caches form. These piles build up until the bottleneck is relieved, at which point workers transfer leaf pieces from the cache into the nest. There are two interesting features of this system. First, it raises the question of how the discrete piles of leaves develop. Second, what is the functional significance of leaf caching?

Ordering and piling behaviours have been studied in other ants. *Pheidole pallidula* makes piles of dead nest-mates (Bonabeau et al. 1998) and *Leptothorax unifasciatus* arranges brood in distinct patterns and locations within the nest (Franks & Sendova-Franks 1992). Positive

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feedback is one of the underlying principles of self-organized systems, such as comb building and foraging trail formation in social insect colonies (Bonabeau et al. 1997). In this study, we tested the hypothesis that cache formation at the entrance of *Atta* nests is subject to positive feedback. Our results show that caches formed only at times of bottleneck and that they developed by the action of positive feedback. Discrete caches also increased the probability that leaf pieces were taken into the nest under laboratory conditions and we suggest further hypotheses to explain the adaptive significance of leaf caching in the field.

METHODS

Study Animals

We studied three colonies of *A. colombica* collected from Gamboa, Panama in March 1998, and two colonies of *A. cephalotes* collected from El Liano, Panama in March 1996. The colonies were housed in climate rooms (25°C, 70% relative humidity) at Aarhus University, Denmark and Sheffield University, U.K. The *A. cephalotes* colonies had ca. 30 000 (colony 1) and 15 000 (colony 2) workers and the *A. colombica* colonies ca. 5000–8000 workers. The entrance to the fungus garden was through a plastic tube 3 cm wide and 15 cm long. During the study, each colony was provided with leaves (*Rubus*, *Prunus*, *Tilia*) as a food source in a box separated from the main nestbox by a 1.5-m wooden bridge.

Testing for Positive Feedback

A colony was provided with leaves and allowed to forage. We placed experimental caches, measuring 4 × 4 cm, on the foraging trail 10 cm from the entrance. The caches consisted of zero, 10, 30 and 80 leaf pieces harvested from incoming foragers within the previous 30 min. The two smaller caches were single layered and the largest cache was multilayered. We observed the first 50 leaf-carrying ants to make physical contact with any part of the leaf pile (or the 4-cm square if the cache size was zero) and recorded the number depositing their leaf piece on the cache. This was repeated 10 times for each cache size per colony. The different cache sizes were presented in random order and there was at least 3 h between the presentation of successive caches.

Leaf Retrieval

We investigated the effect of caching on the rate and probability of leaf retrieval by presenting colonies with 50 scattered or cached leaf pieces. Cached leaves were placed in a square of 4 × 4 cm, 10 cm from the nest entrance and scattered leaves were randomly placed in a square of 30 × 30 cm around the nest entrance. We measured the time taken for the ants to retrieve these pieces. To determine retrieval probability, we used 150 pieces and recorded the number left after 60 min. We presented 43 trials of each type to *A. cephalotes* and 20 trials of each

type to *A. colombica*. As above, the different cache sizes were presented in random order and there was at least 3 h between the presentation of successive caches.

We analysed the positive feedback data with one-way and two-way ANOVAs using Minitab 12.2 for Windows, with cache size and species as factors. A general linear model, rather than a balanced ANOVA, was used because fewer data were collected for *A. cephalotes* than for *A. colombica* ($N=20$ for each cache size for *A. cephalotes* versus $N=30$ for *A. colombica*). P values are two tailed, unless stated otherwise.

RESULTS

General Observations

Ants cached only if there was a bottleneck to the movement of leaf pieces into the nest. This was visible as a blockage of leaves in the entrance tube or a build-up in the fungus gardens. In more than 300 trials ants never cached leaves near the nest entrance when they were able to enter the nest freely.

Positive Feedback

The probabilities of ants dropping leaves were transformed (arcsine square root) and the transformed values used for the two-way ANOVA. There were no significant differences between colonies within species (one-way ANOVA: NS for comparisons between colonies of the same species for each cache size). Consequently, we combined the data for colonies within each species and we used the combined data for the analysis. There was a highly significant effect of cache size on the probability of ants dropping leaves for each species, with the probability of leaf dropping increasing as cache size increased (two-way ANOVA: $F_{3,194}=166.32$, adjusted mean squares=1.688, $P<0.001$). There was no significant difference between the probability of leaf dropping for *A. cephalotes* and *A. colombica* (two-way ANOVA: $F_{1,194}=3.24$, adjusted mean squares=0.328, NS). There was no significant interaction between species and cache size (two-way ANOVA: $F_{1,194}=1.56$, adjusted mean squares=0.016, $P=0.2$). Because there was no difference between species, we combined the data for both species to test for a relationship between cache size and leaf dropping probability. There was a positive relationship between the size of a leaf cache and the proportion of ants dropping leaves (Spearman rank correlation: $r_s=0.791$, $N=201$, $P<0.001$; Fig. 1).

Leaf Retrieval

For each species, we combined the colony data and used the combined data for the analysis. For both species, scattered leaves were retrieved significantly faster than cached leaves (time to recover 50 leaves: *A. cephalotes*: scattered leaves: $\bar{X} \pm \text{SD}=380.2 \pm 99.9$ s, $N=43$; cached leaves: 493 ± 117 s, $N=43$; Mann–Whitney test: $Z=-6.31$, $P<0.001$; *A. colombica*: scattered leaves:

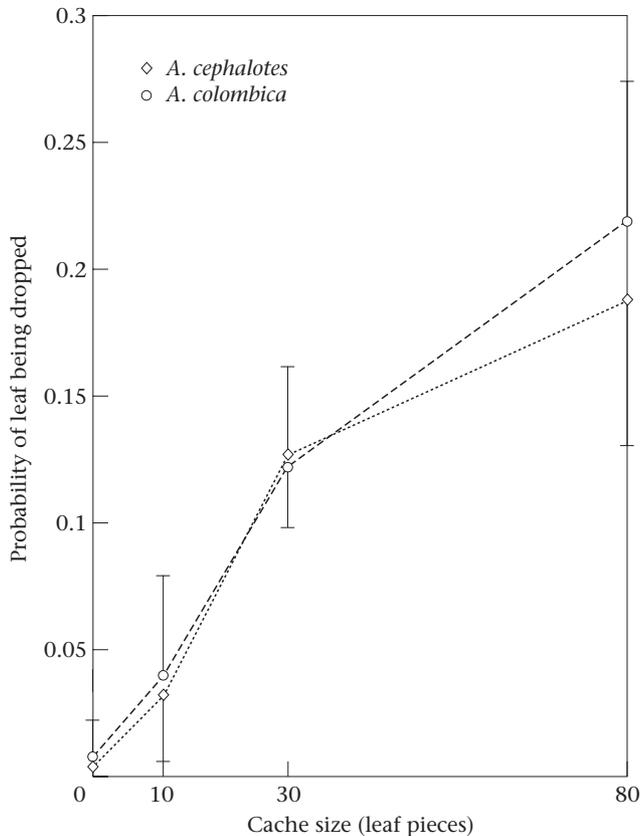


Figure 1. The probability of an ant dropping a leaf in relation to the number of leaves in the cache. The error bars are standard deviations of the proportion cached in different trials.

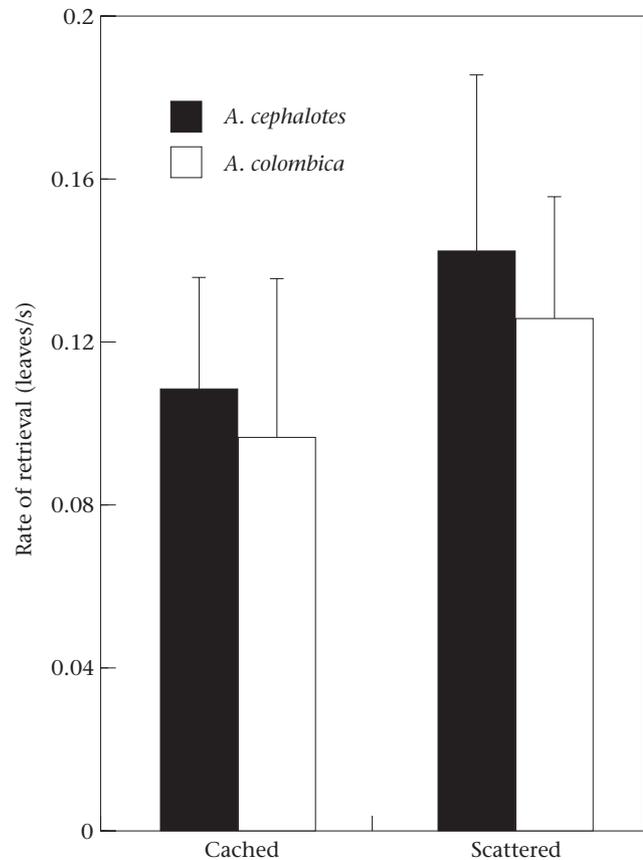


Figure 2. The retrieval rates ($\bar{X} \pm SD$) of 50 cached or scattered leaves.

942 \pm 322 s, $N=20$; cached leaves; 1218 \pm 427, $N=20$; Mann–Whitney U test: $U=275$, $N_1=N_2=20$, $P<0.05$; Fig. 2). Conversely, a greater proportion of cached than scattered leaves was retrieved after 60 min for both species (number remaining after 60 min: *A. cephalotes*: scattered: $\bar{X} \pm SD=17.47 \pm 8$ leaves, $N=20$; cached: 2.3 \pm 3.06, $N=20$; Mann–Whitney U test: $U=391.5$, $N_1=N_2=20$, $P<0.001$; *A. colombica*: scattered: 42 \pm 19.3, $N=20$; cached: 17.5 \pm 17.2, $N=20$; Mann–Whitney U test: $U=335$, $N_1=N_2=20$, $P<0.001$; Fig. 3).

DISCUSSION

Leaf caches in *Atta* ants in our study built up through the action of positive feedback. There was a significant positive relationship between the number of leaf pieces in a cache and the probability of foragers dropping leaves when there was a bottleneck. Returning foragers transferred their leaf pieces to workers inside the fungus garden. If the rate at which leaves arrived exceeded either the processing rate or the rate of worker flow into the nest, then a blockage of foragers and leaf pieces built up in the entrance. This prevented foragers entering the nest and nest entrance caching began (A. G. Hart, personal observation). Foragers initially ‘queued’ outside the nest entrance but then dropped their leaf pieces and returned to the foraging trail. The developing piles of leaves acted

as a focal site for further deposition and consequently the dropped leaves formed a discrete pile. However, the developing cache did not convey the message ‘the nest is blocked, deposit leaves here’. Returning foragers were never observed caching before attempting to enter the nest. Thus, the cache itself was not a releaser of caching behaviour, but organized leaf dropping into discrete areas when the decision to drop had been made. This is comparable to other studies of piling and sorting behaviour (e.g. brood: Franks & Sendova-Franks 1992; dead nestmates: Bonabeau et al. 1998). Leaf caches have been observed in field colonies within nest entrance tunnels, at trail junctions and around obstacles (A. N. M. Bot & U. G. Mueller, personal observation). We suggest that ants should be studied under field conditions to determine whether positive feedback occurs and whether caches act to release caching behaviour.

Positive feedback acts in caching but what adaptive function does it serve? Our study shows that caching increased the probability of leaf retrieval in laboratory colonies. The increase in leaf retrieval probability was small, however, and this result may be an artefact of using laboratory colonies kept in unnatural conditions. Whilst caching increased retrieval probability it also reduced the rate of retrieval perhaps through the effect of mutual interference on the leaf pile. As with retrieval probability, however, the effect on recovery rate was small and could be an artefact. However, in the field, the area around the

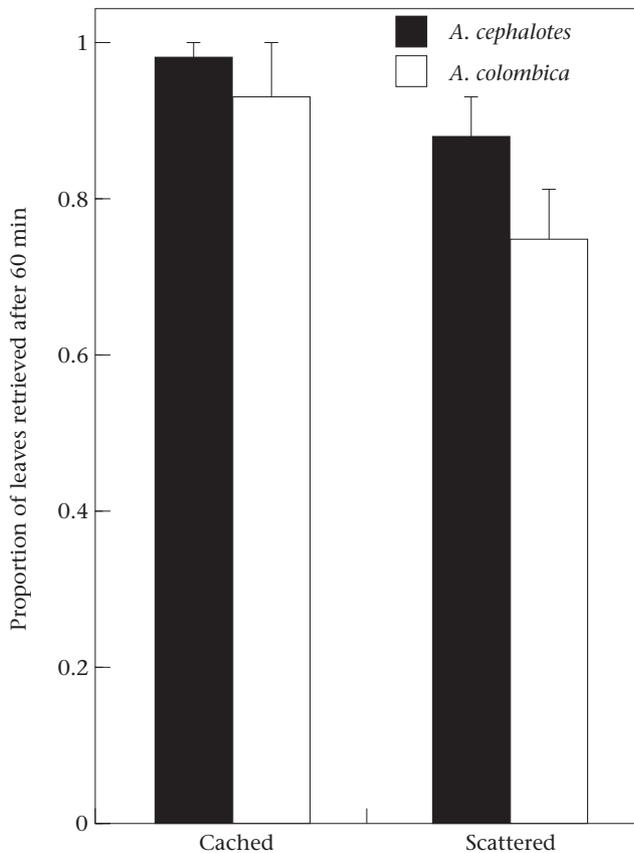


Figure 3. The proportion (\bar{X} +SD) of 150 cached or scattered leaves retrieved after 60 min.

nest is similar to that in our laboratory conditions, that is, bare and flat. Both retrieval probability and recovery rate need to be tested in the field but our study provides the a priori hypothesis that caching does increase retrieval probability.

Nest entrance caching (and caching generally) may serve other functions than temporary storage. The formation of caches at foraging trail junctions may be adaptive in that it allows foragers to return quickly to a new food source and reinforce the pheromone trail (Hubbell et al. 1980). Vasconcelos & Cherrett (1996) showed that leaves might be deposited outside the nest entrance for toxicological reasons. If forage contains substances repellent to the fungus garden then leaves can be left outside the nest to wilt and dry in the air to reduce any toxicological effects. However, this is not a valid explanation for nest entrance caching in our study because the food plants used were nontoxic and were incorporated immediately into the fungus garden in the absence of a bottleneck. Leaf caches forming in pools of water on the foraging trail may also be used as temporary pontoons to allow foragers to cross the pool. However, these accumulations may be mechanistically different from obstacle or junction caches, since it appears that the fragments are not retrieved (U. G. Mueller, personal communication). Field studies are required to determine the full adaptive significance of leaf caching.

Nest entrance caches can be thought of as an adaptive and flexible response. It is probably impossible for a colony to balance forage input with the processing rate of workers in the fungus garden. If the balance tips in favour of forage influx then a bottleneck develops. A worker faced with such a bottleneck queues for a period (possibly dictated by the duration of each foraging foray) and drops its leaf piece. This is a good strategy because if bottlenecks are transitory it gives foragers a chance of entering the nest but does not waste too much time in queuing. This also applies to foragers encountering obstacles on the trail. Leaf pieces can be dropped and recovered later, while foragers can return to the leaf source. However, just dropping leaves on the trail is a costly strategy if the probability of leaf retrieval is low, and this cost increases as the investment in each leaf piece increases. Consequently, if caching has the advantage of increasing retrieval probability, it can enable a colony to minimize the energetic losses associated with mismatched foraging and processing rates. Such ergonomic benefits may be complemented by other benefits such as leaf detoxification or makeshift bridges across temporary water bodies. Further study of leaf caching in the field, both at the nest entrance and on the foraging trail, would result in a more thorough understanding of the sophisticated organization of foraging.

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