Conditioning of scouts and recruits during foraging by a leaf-cutting ant, *Atta colombica*

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Abstract. Experiments using novel and familiar resources were conducted on colonies of the leaf-cutting ant, *Atta colombica* Guerin, in Costa Rica to determine the effects of prior experience on acceptability of plant resources. Two plant species, *Aphelandra golfodulcensis* and *Caryocar costaricense*, grew in the foraging territories of some but not all colonies tested. Artificial patches containing flowers of one or both species were presented to all colonies to study behaviour patterns of scouts and recruits, respectively. Scouts were significantly faster to show recruitment behaviour when encountering a patch containing familiar rather than unfamiliar resources. Workers recruited to a mixed patch by a single scout preferentially harvested resources encountered during travel on trails, regardless of the resource carried by the scout. Colonies treated the two resources differently when they were unfamiliar, accepting *Caryocar* but not *Aphelandra* after a delay of up to 24 h. This difference may be due to inherent differences in acceptability of the two resources. Colonies naturally harvesting *Aphelandra* continued to harvest this resource from artificial patches even after 48 h of exposure to *Caryocar*, suggesting that familiarity altered the relative ranking of the two resources. The results suggest that conditioning affects relative acceptability of resources to both scouts and recruits, and may be a partial explanation for the diversity of resources harvested by ant colonies.

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Prior experience with resources affects subsequent patterns of resource use in many phytophagous insects (Papaj & Prokopy 1989; Szentesi & Jermy 1990). Feeding experience may alter the relative ranking of food resources (Stride & Straatman 1962; Jermy et al. 1968; Phillips 1977; Greenblatt et al. 1978; Barbosa et al. 1979; Schweissing & Wilde 1979; Aboul-Nasr et al. 1981; Flowers &

Yamamoto 1982; Saxena & Schoonhoven 1982; de Boer & Hanson 1984), or promote the use of a restricted subset of available resources (Yamamoto 1974; Cassidy 1978; Dethier 1988; Karowe 1989). Because many social insect species use recruitment to exploit food resources, the effect of experience on decisions made by scouts and by recruits at different stages in the recruitment process can be important for understanding colony-level patterns of resource use. The intensity of recruitment by scouts varies not only in relation to resource location, quantity and quality (von Frisch 1967; Hölldobler 1976; Jaffe & Howse 1979; Crawford & Rissing 1983; Breed et al. 1987), but also according to the prior experience of the scout worker (Raveret-Richter & Waddington 1993). The extent to which recruits make independent decisions during foraging can

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reveal much about the integration of individual behaviour patterns into complex and efficient foraging systems.

The effect of experience on foraging by leaf-cutting ants of the genera *Atta* and *Acromyrmex* is of particular interest because of their dependence on harvesting plant material, on which they culture a fungal symbiote (Weber 1972). Odour cues derived from plants alter resource use in honey bees, *Apis mellifera* (von Frisch 1967; Free 1969, 1970) and other ant species (Jaisson 1980), and might be expected to have a strong influence on leaf-cutting ant behaviour patterns. In fact, workers of the grass-cutting ant *Acromyrmex lundi* can be conditioned to odours of burdens encountered during recruitment (Roces 1990). In this study we investigated the effects of prior experience with plant resources on the behaviour patterns of scouts and recruits, and the consequences for patterns of plant harvest by colonies of the leaf-cutting ant *Atta colombica* Guerin.

Several characteristics of *Atta* foraging systems suggest that experience may play an important role in foraging. Resources used by colonies are distributed unpredictably in space and time; many leaves are acceptable for only part of the year, and flowers or fruit are produced seasonally (Rockwood 1975, 1976). Because individual workers live about 4–6 months (Fowler et al. 1986) resources that are only seasonally available will often be completely novel to foragers. Colonies use long-lived trunk trails to exploit resources (Weber 1972), and both scouts and recruits travelling on these trails gain information from exposure to the burdens carried by returning workers (Jaffe & Howse 1979; Roces 1990). Scouts recruit other foragers directly from peripheral trails (Hubbell et al. 1980), where prior exposure to resources already being harvested may affect the assessment of new resources discovered by scouts. Finally, both colonies (Howard 1987) and individual workers (Therrien 1988) differ in preference rankings of simultaneously presented, acceptable resources.

These considerations led us to advance two hypotheses regarding the role of experience in foraging. First, we hypothesized that prior exposure to plant resources would alter the propensity of scout ants to recruit other workers after locating a potential food source. We predicted that scouts encountering a familiar resource would more rapidly accept it and recruit other workers than when encountering an unfamiliar resource. Second, based on the results of Roces (1990), we hypothesized that conditioning to burdens encountered during recruitment would alter the relative acceptability of resources to recruits. Specifically, we predicted that workers would more readily accept resources encountered during recruitment by a scout than acceptable alternatives not encountered during recruitment.

MATERIALS AND METHODS

We studied six colonies of *A. colombica* in Corcovado National Park, Costa Rica, within 0.5 km of park headquarters in Sirena. Experiments took place from 28 February to 2 March 1993, during the dry season when fallen flowers are major resources for the ants. We investigated the responses of scouts and recruits to two highly acceptable resources that varied in novelty to colonies; fallen flowers of *Aphelandra golfodulcensis* (Acanthaceae) and *Caryocar costaricense* (Caryocaraceae). *Aphelandra* grew within the foraging territories of two colonies, but was absent from a radius of at least 150 m around the other four colonies. *Caryocar* grew within the foraging territories of two other colonies, and did not grow within 300 m of the other four colonies. The final two colonies had access to neither floral resource, and foraged primarily on fallen stipules of *Ficus insipida* (Moraceae), which occurred within the territories of all colonies. In this paper we refer to these as *Aphelandra*, *Caryocar*, and *Ficus* colonies respectively.

We conditioned ants to flowers presented in artificial patches to examine ant responses to novel and familiar resources. On the morning of 28 February we established patches consisting of 20–50 g of a single resource scattered over about 0.1 m², within 20 cm of an existing trunk trail, and at least 20 m from the colony. These patches were maintained for the next 48 h, and flowers replenished as they were depleted by the ants. Patches not used by the ants were replenished twice a day with fresh flowers, and any unused flowers were discarded. We established patches on two different trails per colony, one patch containing *Aphelandra* and the other patch containing *Caryocar*. For each colony we selected trails whose foraging was dominated by a single resource. Trails selected from *Aphelandra* and *Caryocar* colonies harvested

these resources exclusively, and *Ficus* stipules consisted of over 90% of burdens on trails selected from *Ficus* colonies.

We distinguished scouts from recruits by their fidelity to existing physical and odour trails. We defined scouts as those ants that spontaneously left trunk trails without following an odour trail left by another ant. These ants wandered slowly and on irregular paths through areas adjacent to trunk trails that lacked any other ant activity. Upon encountering an acceptable resource, these ants cut a piece and returned to the trail while touching the gaster to the ground, presumably laying odour trails. Recruits were defined as those ants that left trunk trails after encountering the odour trail laid by a scout, and directly followed the odour trail to a resource patch.

We examined the willingness of scouts to accept novel and familiar resources by determining the length of time required after initially encountering a patch for a scout ant to cut a piece, return to the trunk trail and attempt to recruit another ant. Recruitment was deemed to have occurred when one to several unladen workers left the trunk trail, following the scout's odour trail towards the patch. Preliminary experiments using common leaves revealed that scout ants encountering artificial resource patches often required 30 min to cut and attempt recruitment. We continuously observed the behaviour patterns of single scouts in all patches for up to 45 min after initial discovery of the patch. We limited our observations of scouts to the first ant to encounter our patches; in only one case did a second ant independently locate a patch without following the odour trail of the first ant to find the patch. This ant was removed to ensure that responses of recruits were not altered by different numbers of scouts. We abandoned direct observation of scout behaviour patterns after 45 min but checked for signs of recruitment activity at hourly intervals for the remainder of the day and every 4 h over the next 48 h.

Eight of the 12 floral patches contained resources novel to the ants, and to obtain a clear picture of ant responses to familiar resources we also determined the reactions of scouts to patches of *Ficus* stipules, a resource harvested by one or more trails of all six colonies. Stipules were placed in separate patches at least 2 m from flower patches, and were continuously monitored for up to 45 min as described above. We used these patches only to study initial reactions of a single scout per patch, and removed stipules after the initial observation period.

We studied the reactions of initial recruits to familiar and novel floral resources immediately after successful recruitment to a flower patch by scout ants, or after 45 min of investigation by scouts. As soon as recruitment was observed, or after 45 min, we removed all flowers from the patch to remove any odour cues left on resources by scouts. We then replenished the patch with an equal mixture of *Caryocar* and *Aphelandra* and tallied the identity of pieces harvested from the patch until 20 pieces had been harvested or until an hour had passed. We stopped observation at this time to reduce the probability that a given ant could revisit the patch, and because ants arriving subsequently might have encountered a substantially different mixture of burdens on the trail than those arriving initially. We then removed the mixture of flowers and restocked the patch with 20–50 g of the resource originally offered.

This experiment allowed us to distinguish between three possible scenarios for the influence of recent experience on recruit behaviour. While travelling on trails, workers encounter hundreds or thousands of burdens prior to encountering the single burden carried by the scout. If simple conditioning has an important impact on ant behaviour, recruits might be expected to show a clear preference for the resource encountered on the trail, because their recent sensory experiences overwhelmingly arose from this source. If conditioning to plant cues is specifically elicited by recruitment behaviour, then recruits should prefer the resource carried by the scout, regardless of which resource dominates the trail. Finally, conditioning might be unimportant relative to an innate preference hierarchy possessed by all ants. If so, recruits might independently evaluate resource characteristics as they are encountered and only follow scouts to locations. In this case all recruits should prefer the same resource, regardless of all other cues.

To examine the behaviour patterns of ants as novel resources became more familiar, we retested each trail with a mixture of flowers after 24 and 48 h, following the procedure outlined above. Patches were essentially continuously occupied by one or more ants after their initial discovery, and we assumed that all ants visiting the patches in these experiments were recruits following

established odour trails. We stopped our experiments after 48 h because three colonies began harvesting new resources on one or both of our study trails; one of the *Ficus* colonies began harvesting fallen *Sapium thelocarpum* leaves, and both *Aphelandra* colonies began harvesting varying amounts of *Ficus* stipules.

RESULTS

Behaviour of Scout Ants

Scout ants showed marked differences in propensity to accept novel and familiar resources (Table I). Scouts encountering *Ficus* stipule patches immediately antennated stipules and in every case began cutting within 10 min of initial encounter. In all cases, scouts attempted to recruit other workers, and all succeeded in attracting one or more workers from the trunk trail within 45 min. Scouts encountering floral resources previously encountered on trails behaved similarly, and recruited other ants within 45 min to three of four patches. Scouts from one *Caryocar* colony located their *Caryocar* patch but did not cut flowers or attempt to recruit until the second day.

Scouts encountering unfamiliar floral resources antennated but generally did not cut the flowers, and in only one of eight patches were other ants recruited within 45 min of discovery. A scout from one *Aphelandra* colony cut *Caryocar* and recruited other ants after 32 min. Scouts from other colonies unfamiliar with *Caryocar* eventually accepted this flower, but only after a full day of exposure in three of four cases. Scouts from colonies unfamiliar with *Aphelandra* never attempted to recruit other workers to *Aphelandra* flowers during the 48 h of the experiment. Because acceptance times were non-normally distributed, we simply scored them as greater or less than 45 min for the purposes of statistical analysis. A Pearson chi-squared test indicated that scout ants more readily accepted familiar resources than unfamiliar resources ($\chi^2=12.5$, $df=1$, $P<0.001$).

Initial Recruitment to Patches and Recruit Behaviour

After initial observations of scout ant behaviour patterns, we removed the conditioning resource from each patch and replaced it with approximately equal masses of *Aphelandra* and *Caryocar* flowers. In one *Aphelandra* and one

Table I. Time required by *Atta colombica* scout ants to accept familiar and unfamiliar resources

Resource	Acceptance time	
	<45 min	>45 min
Ficus stipules (familiar)	8	0
Familiar flowers	3	1
Unfamiliar flowers	1	7

Familiar resources (stipules and flowers combined) are more rapidly accepted than unfamiliar resources ($X^2=12.5$, $df=1$, $P<0.001$).
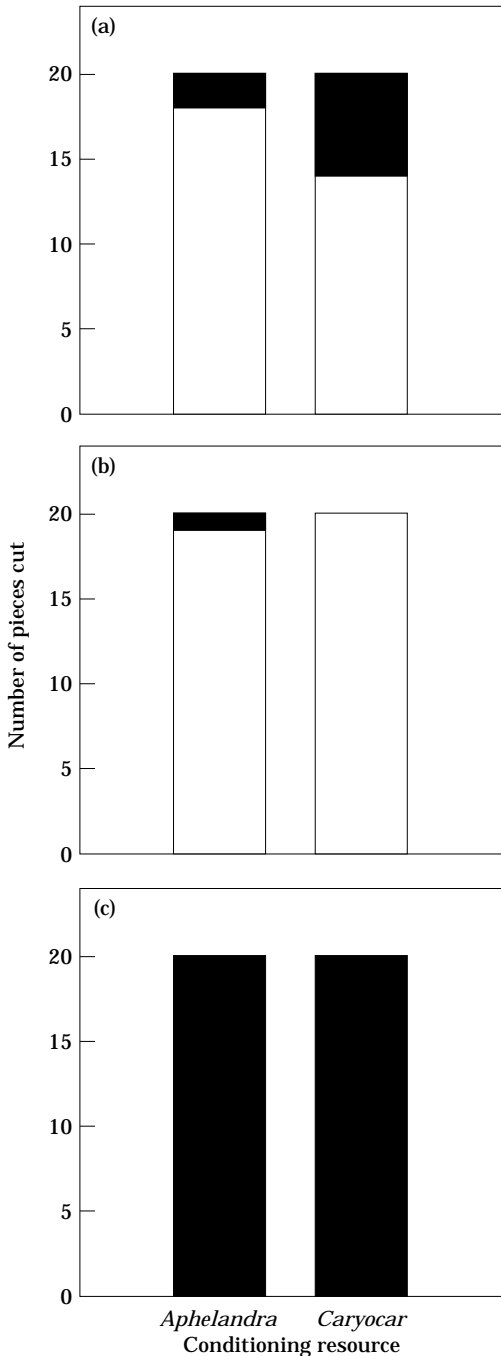
Caryocar colony, scout workers that had initially failed to accept unfamiliar resources immediately began cutting the familiar resource already being harvested by the trail, and recruited other workers to these patches. The second *Caryocar* colony and both *Ficus* colonies continued to ignore both patches.

In the three colonies displaying immediate recruitment to patches, recruited workers clearly preferred resources encountered on trails during their outward journey (Fig. 1). Workers from *Aphelandra* colonies harvested a high proportion of *Aphelandra* flowers, regardless of which flower had been initially presented in a patch, but those from the single *Caryocar* colony showing recruitment harvested only *Caryocar* flowers. Workers from the two *Aphelandra* colonies harvested only small amounts of *Caryocar*, even though they had in one instance been recruited by a scout carrying *Caryocar*.

Resource Use and Colony Experience

All colonies visited *Caryocar* patches after 24 h, establishing branch trails and in some cases entirely depleting patches during the 4 h intervals between checks. One *Caryocar* colony showed only minimal interest in our artificial patches, probably due to the large quantities of fallen *Caryocar* flowers available to this colony. This colony foraged diffusely, maintaining only weak trails with much lower activity than any other colony (mean ± SD = 14.2 ± 9.5 (N=6) versus 42.4 ± 24.4 (N=29) ants/min). *Aphelandra* colonies similarly used *Aphelandra* patches, but other colonies entirely ignored these patches. Scout ants had clearly investigated all patches, because ants rapidly recruited to all patches when both flowers were simultaneously presented at 24 and 48 h.

Colonies showed strong differences in resource use when offered mixtures of the two resources after 24 and 48 h of conditioning. *Caryocar* and *Ficus* colonies virtually ignored *Aphelandra*

flowers during these experiments, regardless of which resource had previously been offered in artificial patches (Fig. 2). In contrast, *Aphelandra* colonies continued to harvest significant amounts of *Aphelandra* after 24 and 48 h of exposure to *Caryocar* (Fig. 2). In addition, *Aphelandra* colonies harvested significantly different proportions of the two flowers from different patch types. In both colonies the proportion of *Aphelandra* pieces cut from patches in which *Aphelandra* was initially presented was significantly higher than the proportion cut from patches initially containing *Caryocar* (χ^2 test; Colony A: $P<0.001$ on both days; Colony B: $P<0.01$ on both days).

DISCUSSION

Scout ants cut pieces and initiated recruitment significantly sooner when encountering familiar resources than when encountering novel resources. Leaf-cutting ants may show longer delays in accepting unfamiliar resources than is typical of most ants, due to the complexity of the cues that must be evaluated by scouts. Wide variation in nutrient content among plant species and diversity of plant secondary compounds present problems of resource recognition and evaluation to plant-harvesting generalist herbivores such as leaf-cutting ants (Dethier 1980; Mattson 1980). In contrast, predators, scavengers and nectar-harvesters use resources consistently rich in protein, lipids or simple sugars. Efficient exploitation of such resources may require a variety of search or capture strategies, but recognition of novel resources as appropriate food generally occurs quickly (Déjean et al. 1993; Fourcassié & Traniello 1994).

Novelty delayed but did not prevent acceptance of *Caryocar* flowers, but novel *Aphelandra* flowers were never accepted during the 48 h of the study. This asymmetry may be due to inherent

Figure 1. Number of *Aphelandra* (□) and *Caryocar* (■) flower pieces harvested by workers recruited by a single scout to artificial patches containing an equal mixture of resources. Scouts initially encountered either *Aphelandra* or *Caryocar* as a conditioning resource in a given patch. (a) and (b) are results for colonies whose trails naturally harvested only *Aphelandra*. (c) Summary of results from a colony whose trails naturally harvested only *Caryocar*.
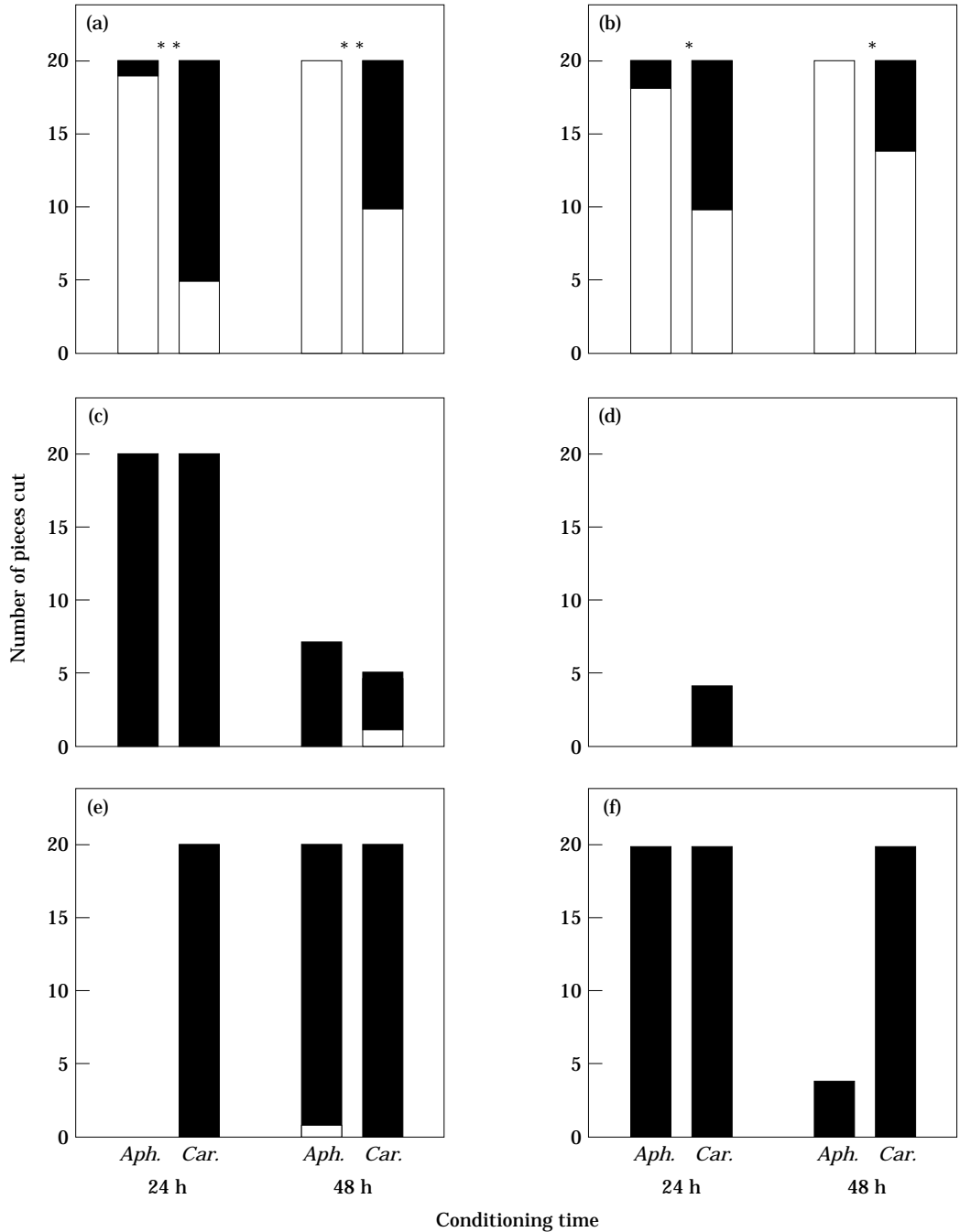
Figure 2. Number of *Aphelandra* (□) and *Caryocar* (■) flower pieces harvested by workers exploiting artificial patches containing an equal mixture of resources, after 24 and 48 h of exposure to one of the two resources. (a), (b) Colonies whose trails naturally harvested only *Aphelandra*; (c), (d) colonies whose trails naturally harvested only *Caryocar*; (e), (f) colonies whose trails naturally harvested >90% stipules of *Ficus insipida* during the 48-h experiment. Colonies (a) and (b), conditioned to *Aphelandra* and *Caryocar*, harvested significantly different proportions of these two resources from mixed patches (χ^2 test: *=$P<0.01$; **=$P<0.001$).

differences in the quality of these two resources. Although *Aphelandra* and *Caryocar* did not generally grow in the same localities, we discovered one colony near Sirena that had access to both floral resources. This colony harvested only *Caryocar*, even though trails passed through patches of fallen *Aphelandra* flowers, and this suggests that *Caryocar* flowers were preferred to *Aphelandra* flowers when both were familiar. The fact that colonies naturally harvesting *Aphelandra* continued to harvest large amounts of this species even after discovery of *Caryocar* suggests that experience altered the relative ranking of these resources.

Contrary to our expectations, the acceptability of resources to recruits was unaffected by cues encountered during recruitment, but was significantly altered by the resource already being harvested. Roces (1990) demonstrated conditioning to odour cues of a single burden carried by a scout ant under highly controlled laboratory conditions, but ants in the field apparently integrate all cues encountered. Ants may gain experience with resources on trails or in the nest, but our results suggest that subsequent conditioning is relatively short term and varies dynamically as a function of number or rate of resource contacts. Once exposed to both resources, *Aphelandra* colonies cut different proportions of *Aphelandra* and *Caryocar* in the two patches (Fig. 2), presumably because recruits encountered a different balance of *Aphelandra* and *Caryocar* burdens on the trails serving the patches.

Conditioning of foragers may promote patterns of resource harvest beneficial to the fungal symbiote of attine ants. Despite the essentially complete preference of *Ficus* and *Caryocar* colonies for *Caryocar* in our tests, colonies naturally cutting *Aphelandra* harvested a mixture of the two resources from *Caryocar* patches (Fig. 2). Conditioning may thus serve as a proximate mechanism promoting a diverse mixture of resources in the diet by maintaining existing resources in the diet even after discovery of new ones. A diverse diet may be beneficial because high-quality patches make up only a fraction of the resources available on a single plant (Howard 1990), and maintaining adequate rates of mass flow may require simultaneous harvest of several different resources. Also, even the most preferred resources may have nutrient deficiencies or contain allelochemicals that make a mixed diet advantageous.

The preference of conditioned recruits for familiar resources may also have important effects on harvesting efficiency. *Atta* colonies may simultaneously maintain several hundred fungus gardens (Weber 1972), which require a high rate of mass flow into the colony. Since some scouts took as long as 45 min to accept even familiar resources, independent assessment of resource suitability by each recruit would be likely to result in far lower rates of mass flow than possible with conditioned recruits. Simultaneous encounter of multiple resources is likely to be a common occurrence, since ants often establish trails on lianas connecting several plants with inter-leaving branches, and conditioning is likely to ensure high rates of mass flow from preferred resources under these conditions. Although conditioning may benefit colonies by increasing efficiency of harvest of existing resources, it may also carry costs by delaying the acceptance and exploitation of new resources. Further investigation of the dynamics of conditioning and its impact on worker behaviour patterns and colony-level resource use would clearly be of value.

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