

Arboreal substrates influence foraging in tropical ants

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Abstract. 1. Physically complex substrates impart significant costs on cursorial central-place foragers in terms of time spent outside the nest and total distance travelled. Ants foraging in trees navigate varied surfaces to access patchy resources, thus providing an appropriate model system for examining interactions between foraging efficiency and substrates.

2. We expected that the speed of recruitment, body size distribution and species richness of foraging arboreal ants would differ predictably among common substrate types occurring on tropical tree trunks. We measured changes in ant abundance and species composition over time at baits placed on bare tree bark, moss-covered bark, and vine-like vegetation appressed to bark. We also measured average body size and body size frequency on the three substrate types. Ants discovered baits sooner and accumulated at baits relatively faster when using vine substrates as the primary foraging trail. Average body size was smaller on vine substrates than on bark. Experimental removal of vine and moss substrates nullified these differences. Contrary to our predictions, species richness and body size distributions did not differ among the three substrate types, due in part to the frequent presence of a few common ground-nesting species at baits on bare bark.

3. Our results collectively indicate that linear substrates facilitate access of foraging ants to patchy resources. Ant use of vine-like substrates appears to be opportunistic; vine use is not confined to certain species nor constrained by body size.

Key words. Costa Rica, Formicidae, resources, tropical forest, vines.

Introduction

For central-place foragers, time and energy costs increase with distance to resources (e.g. Orians & Pearson, 1979; Schoener, 1979; Stephens & Krebs, 1986). For cursorial central-place foragers such as ants, costs also increase with habitat complexity, in part because obstacles lengthen the three-dimensional path to a resource patch and reduce overall velocity (e.g. Fewell, 1988; Sponberg & Full, 2008). Distance and velocity determine the frequency of exposure to predators, competitors, environmental hazards, and other factors potentially affecting the rate of energy flow into the nest (e.g. Detrain *et al.*, 1999; Denny *et al.*, 2001; Yunger *et al.*,

2002; Devigne & Detrain, 2006; Dornhaus & Powell, 2010). Consequently, central-place foragers are expected to maximise efficiency by selecting low-resistance pathways whenever possible (Fewell, 1988; Torres-Contreras & Vásquez, 2004; Farji-Brener *et al.*, 2007).

A forager's perception of environmental complexity depends on the interaction between substrate properties and its body size, morphology, and gait (Kaspari & Weiser, 1999; Parr *et al.*, 2003). For example, as a result of characteristics of their gait, the running velocity of some cursorial arthropods may be unaffected by relatively significant substrate heterogeneity (Sponberg & Full, 2008). Likewise, the spacing of obstacles such as trichomes may determine the navigability of plant parts to ants based on their body size (Davidson *et al.*, 1989). Unfortunately, substrate properties (e.g. surface roughness) and the spatial arrangement of obstacles can be challenging to quantify at scales relevant to insects and other common central-place foragers, especially under field conditions. Here

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we examine the effects of grossly different natural substrate types on foraging behaviour, body size distribution, and species composition using tropical arboreal ants as a model system.

As ants are embedded in a broad range of ecological processes (e.g. herbivory, seed dispersal, and mutualisms), understanding their behavioural ecology and foraging methods is relevant to understanding the functioning of tropical rain forest ecosystems as a whole. Ants are easily observed and account for a large fraction of the abundance and biomass of arthropods associated with tropical trees (e.g. Tobin, 1995; Davidson *et al.*, 2003); they show broad variation in body size within and among genera (e.g. Kaspari & Weiser, 1999); and they are ecologically important (e.g. Hölldobler & Wilson, 1990; Lach *et al.*, 2010). Ecological associations between ants and plants are well documented (Beattie, 1985; Rico-Gray & Oliveira, 2007), but less is known of the potential connections between forest structure (e.g. liana abundance; Phillips *et al.*, 2005) and ant ecology.

Arboreal ants (defined for this study as ants that use above-ground vegetation as primary foraging substrates) navigate over or through a variety of surfaces, including bark of varying rugosity, moss, lichens, stems, and leaves. Many species may inhabit a single tropical tree (e.g. Wilson, 1987; Tobin, 1995; Scultz & Wagner, 2002), and the linear nature of the canopy environment promotes aggressive interactions and territoriality (e.g. Hölldobler & Lumsden, 1980; Davidson, 1997; Yanoviak & Kaspari, 2000). Arboreal ant assemblages tend to be organised into dominance hierarchies (e.g. Savolainen & Vepsäläinen, 1988), and it is possible to observe interactions among potentially competitive ant species by placing a highly desirable bait within their foraging territory (e.g. Kaspari & Yanoviak, 2001). Although forest canopies are linear habitats by first-order approximation, smaller-scale substrate properties (e.g. trichomes; Davidson *et al.*, 1989) and the presence of different structural components (e.g. vines; Bentley, 1981) may mediate interactions among ants based on body size.

Vines and lianas occur on most trees >10 cm diameter in tropical forests (Kurzel *et al.*, 2006) and are ecologically important elements of forests worldwide (e.g. Putz, 1984; Schnitzer & Bongers, 2002; Phillips *et al.*, 2005; van der Heijden *et al.*, 2008; Cai *et al.*, 2009). Our observations at various lowland Neotropical sites suggest that ants preferentially use vines as foraging pathways, functioning similarly to the fallen branches used by ants traversing the forest floor (Farji-Brener *et al.*, 2007). As part of a larger investigation of the ecological links between lianas and ants, the principal goal of the present study was to determine if use of vine-like pathways facilitates efficient foraging by arboreal ants.

We hypothesised that differences among common tree trunk substrates are reflected in patterns of foraging behaviour by tropical arboreal ants. We made three predictions. First, because vines provide relatively direct, unobstructed, defensible access routes to food patches, ants foraging on tree trunks will accumulate faster on baits adjacent to appressed vines versus baits on bare bark or moss-covered bark. Second, as complex substrates are likely to impede locomotion specifically in mid-sized ants (Kaspari & Weiser, 1999; Yanoviak & Kaspari, 2000), the body size of behaviourally dominant ants will be

bimodal on moss substrates and unimodal on appressed vines. Finally, given that aggressive interactions may be more intense on linear substrates (Yanoviak & Kaspari, 2000), we expect species richness of ants on resources associated with vines to be lower than on bark or moss substrates. We employed a combination of observational and experimental bait studies to test these predictions in a lowland Neotropical forest.

Materials and methods

Field work was conducted at the La Selva Biological Station, Costa Rica (10.43°N, 84.00°W) in June and July of 2006 and 2007. The site is dominated by lowland wet tropical forest and receives *c.* 4000 mm of rain per year (McDade *et al.*, 1994). All field observations were completed between 09.00 and 15.00 hours during fair weather.

We selected 45 trees ranging from 35 to 100 cm in diameter at breast height and within 5 m of trails in old growth forest. Focal trees were >10 m apart and were not identified to species; rather, we chose trees with a relatively smooth bark and readily accessible, closely-approximated patches of three common trunk substrates: (i) bare bark; (ii) mossy-liverwort growth; and (iii) bare bark with isolated appressed vines, lianas or hemiepiphyte roots. Hereafter, we refer to these substrates as *bark*, *moss*, and *vine*, respectively. Focal patches on each tree trunk were >500 cm² and 1–2 m above the ground. The ‘vine’ substrates ranged from 4 to 10 mm in diameter, were smooth and free of epiphytic cover, and extended at least 3 m up the trunk from the point of observation. ‘Moss’ depth was >3 mm (measured orthogonal to the trunk surface with calipers). We recorded temperature in the shade at the midpoint of each replicate time series.

We used canned tuna (in water) mixed with honey as bait to attract ants. Three baits of equal size (*c.* 6 cm², 5 g wet weight) were placed directly on a tree trunk, one in each of the three focal patches. We recorded the number of ants and the number of ant morphospecies on each bait at 1, 2, 4, 8, 16, 32, and 64 min after placement. At the end of a trial, representative samples of ants were collected with forceps and stored in 90% ethanol for later identification.

Bait locations were marked with insect pins and flagging, and the baits were removed. All vegetation was scraped from the moss patch to create a bare bark area of >10 cm radius around the prior bait location. Likewise, all vine-like substrates were removed from the vine patch from ground level up to approximately 2 m above the prior bait location. As a control, an equivalent area associated with the bait location in the bare bark patch was rubbed by the investigator. The tree was left undisturbed for >4 days and then re-baited at the same locations. Ants again were observed over a logarithmic time series up to 64 min, and other variables were recorded as described above.

Collected ants were identified to species or morphospecies using keys and online resources (e.g. Bolton, 1994; Longino, 2009). Worker body size for each species was determined by measuring overall length (from clypeus to abdominal apex) using digital calipers or an ocular micrometer. We used media workers to represent the body size of polymorphic species.

Vouchers were deposited at INBio (San Jose, Costa Rica) and in the first author's private collection.

We analysed differences in average absolute abundance and relative abundance of ants (i.e. the proportional distribution of ants among baits at each observation period) among substrate types over time with repeated-measures ANOVAs. We used one-way ANOVAs and *post hoc* Tukey tests to compare the average time to bait discovery (the interval from bait placement to the appearance of the first ant) and the maximum

number of ants present at a bait among substrates before and after experimental manipulations. Baits with only one ant present during the observation period (i.e. no recruitment) were excluded. We similarly tested for differences in the cumulative number of visiting species (species richness) and the average body size of behaviourally dominant ants at baits. We defined dominance behaviour as recruitment leading to nearly exclusive occupancy of a bait, or active defence of a bait (Yanoviak & Kaspari, 2000; Parr & Gibb,

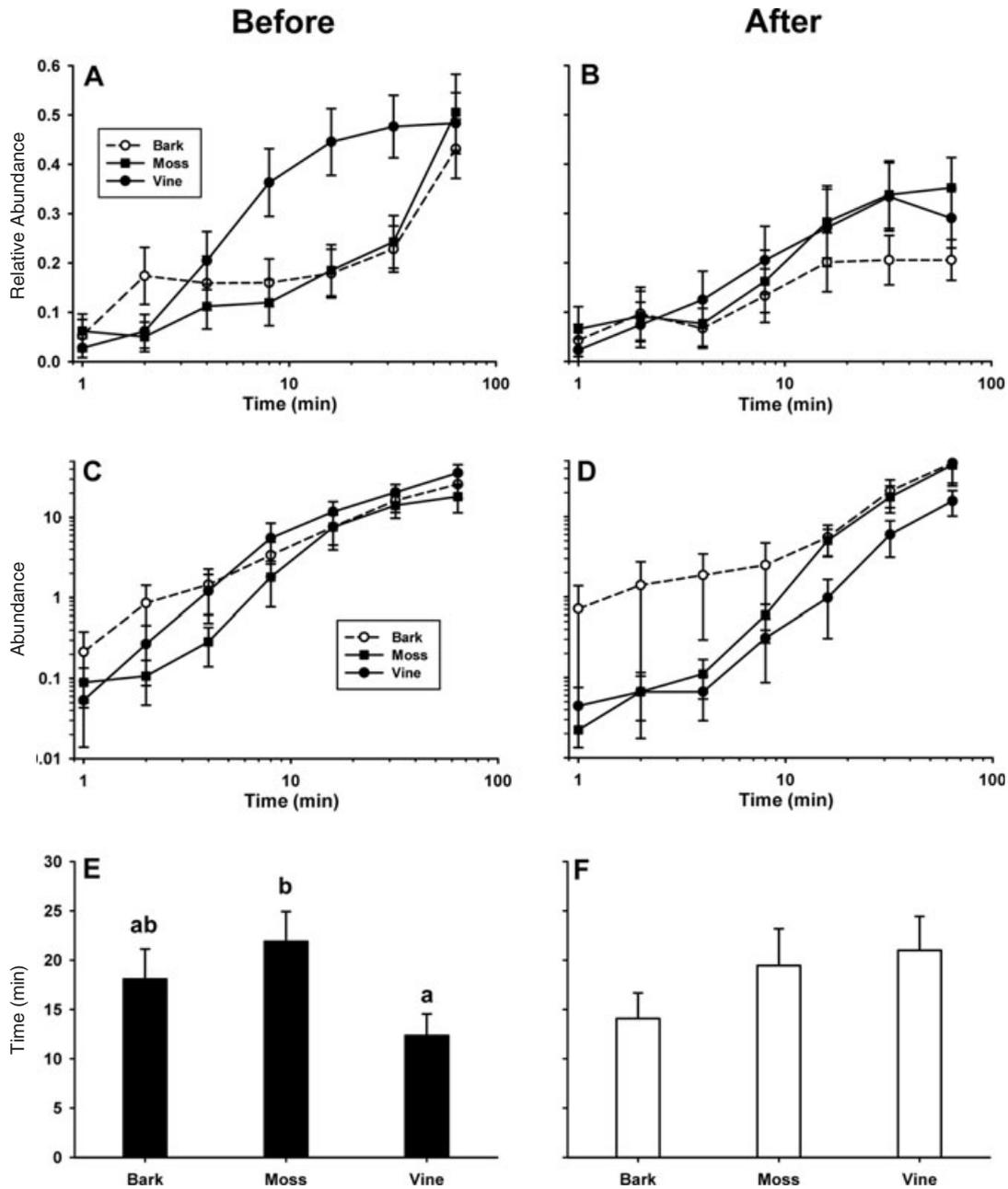


Fig. 1. Comparison of average (\pm SE) relative abundance of ants (A, B), absolute abundance of ants (C, D), and bait discovery time (E, F) on three different substrate types before and after vine and moss substrates were experimentally removed. Similar lower case letters in (E) indicate means that do not differ; all means in (F) are statistically similar.

2010). We used paired *t*-tests with Bonferroni's adjustment to compare foraging parameters within a substrate type for baits that were visited both before and after experimental removal. Data from 2006 and 2007 field seasons were combined for all analyses except those depending on accurate species richness or composition data, as some of the 2006 samples were positively identified to genus only. Abundance and time data were $\log_{10}(x + 1)$ transformed, and proportional data were arcsine-square root transformed before analysis (Sokal & Rohlf, 1995). All analyses were conducted with SAS 9.1 (SAS Institute, 2002).

Results

We observed *c.* 6000 ants representing 30 morphospecies visiting baits during the study. Approximately 25% of the morphospecies visiting baits were ground-nesting taxa that

facultatively forage on understory portions of tree trunks. Total ant abundance at baits was not correlated with temperature ($\rho = 0.13$, $P = 0.49$), which ranged from 25.2 to 30.5 °C during bait trials. Ant abundance generally increased at baits during the observation periods (Fig. 1).

As we predicted, the average relative abundance of ants was greater on baits associated with vine substrates than moss or bark substrates over time (Fig. 1; $F_{2,90} = 3.51$, $P = 0.032$; Table S1). Average absolute abundance did not differ among substrate types (Fig. 1; $F_{2,90} = 2.28$, $P = 0.108$; Table S2), but was larger on vine baits than on moss baits when the bark treatment was excluded ($F_{1,60} = 5.86$, $P = 0.019$). Patch discovery time (time to first ant on a bait, with subsequent recruitment) was shorter on vine substrates than moss substrates ($F_{2,97} = 3.19$, $P = 0.045$; Fig. 1). The average body size (length) of the dominant ants was smaller on vines than on bark ($F_{2,72} = 4.77$, $P = 0.011$; Fig. 2), but contrary to our

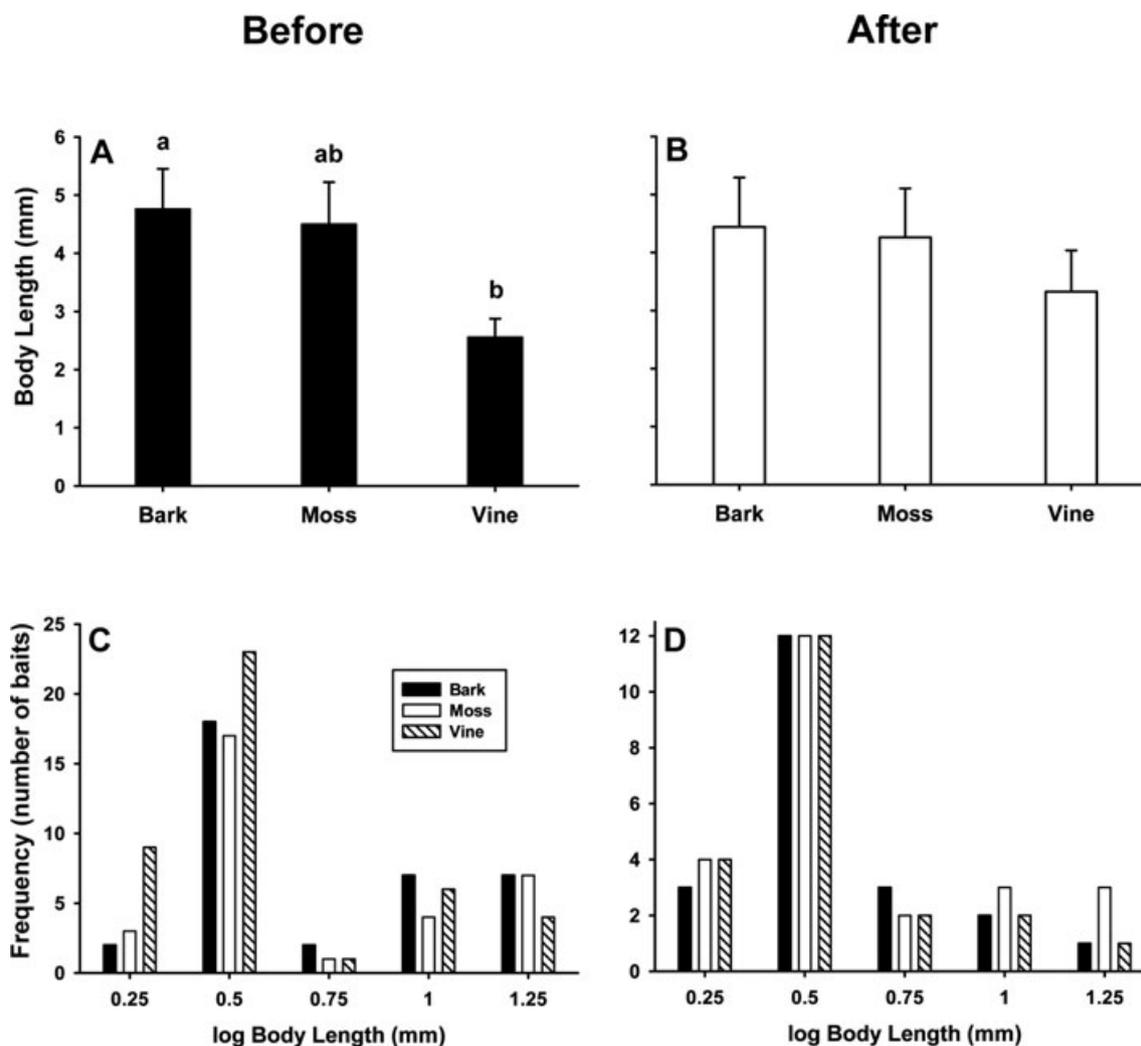


Fig. 2. Comparison of average (\pm SE) body size of ants (A, B) and frequency of bait occupancy by different size classes of ants (C, D) on three different substrate types before and after vine and moss substrates were experimentally removed. Similar lower case letters in (A) indicate means that do not differ; all means in (B) are statistically similar.

prediction, the frequency distribution of ant body size at baits was similarly bimodal among all substrate types (Fig. 2).

We observed two patterns in ant foraging behaviour that were particularly relevant to the objectives of this study. First, ants sometimes initially established foraging trails to vine baits via a non-vine pathway (i.e. over bare bark). In almost every case, these ants subsequently shifted their foraging trail to include the vine. Second, bark and moss baits were occasionally overtaken by dominant ants that had first established control of vine baits. We did not observe similar trail shifts or expansion to other baits for ants that initiated foraging on moss or bark baits.

Baits associated with vines were not visited by fewer species as expected; average species richness at baits was similar for all substrates (range = 0–3 species; $F_{2,90} = 1.23$, $P = 0.30$). *Solenopsis*, *Pheidole*, and *Ectatomma* were the most frequently encountered genera overall, each visiting ≥ 6 baits per substrate type. Other genera found at baits on all substrates included *Paratrechina*, *Dolichoderus*, and *Pachycondyla*. Cumulatively, more genera visited bark baits (12) than moss (8) or vine (9) baits. Whereas there was considerable overlap in taxonomic composition of the common ants on vine and moss substrates, several taxa foraged exclusively at bark baits. These included arboreal nesting species (e.g. *Camponotus senex*, *Gnamptogenys annulata*, *Odontomachus* spp., and *Pachycondyla* spp.), as well as ground-nesting ants (e.g. *Aphaenogaster araneoides*) that occasionally forage on tree trunks in the understory. *Brachymyrmex* was the only genus found exclusively on vine baits. *Ectatomma ruidum* frequently displaced preexisting species when foraging, and abundant *Pheidole* spp. and *Solenopsis* (*Diplo.*) spp. regularly swarmed baits, subsequently excluding secondary species.

Experimental removal of substrates strongly influenced many of the quantitative patterns described above. Specifically, the relative abundance of ants at baits ($F_{2,42} = 1.88$, $P = 0.16$; Fig. 1), bait discovery time ($F_{2,65} = 0.67$, $P = 0.52$; Fig. 1), and ant body size ($F_{2,48} = 0.55$, $P = 0.58$; Fig. 2) did not differ among substrate types after removal. Likewise, the distribution of ant body size at baits tended towards unimodality after the manipulation (Fig. 2). Subsequent paired analyses showed that effects of substrate removal were strongest for baits associated with vines. Specifically, vine removal caused an increase in average bait discovery time and ant accumulation rate, and a decrease in the average maximum number of ants at a bait (Table 1). In contrast, manipulation of moss and bark substrates had no effect on these parameters (Table 1).

As observed before the substrate removal, 0–3 species occurred at each bait after the manipulation and average ant species richness did not differ among the three substrates ($F_{2,90} = 0.15$, $P = 0.86$). Likewise, *Ectatomma*, *Paratrechina*, *Pheidole*, and *Solenopsis* were the most common and often behaviourally dominant genera at baits. The four genera previously observed only at bark baits (see above) also visited vine and moss baits after those substrates were removed. There was a strong tendency for *Solenopsis* spp. to subsequently dominate baits that were controlled by *Pheidole* spp. before the manipulation. This pattern did not vary among bait locations

Table 1. Characteristics of ants and their foraging patterns on baits before and after substrates were experimentally removed.

	Substrate	Before	After	t
Discovery time (minutes)	Bark	11.5 ± 3.66	15.5 ± 3.19	1.42
	Moss	16.6 ± 4.15	17.2 ± 4.04	0.34
	Vine	10.5 ± 2.21	23.1 ± 3.77	2.49*
Accumulation rate (ants per minute)	Bark	2.0 ± 0.57	2.0 ± 0.52	0.10
	Moss	2.7 ± 0.81	1.9 ± 0.52	0.17
	Vine	1.5 ± 0.30	1.0 ± 0.28	3.00**
Max. abundance	Bark	47.9 ± 16.99	66.5 ± 27.38	1.03
	Moss	38.5 ± 13.41	56.7 ± 25.40	0.82
	Vine	50.7 ± 10.53	16.1 ± 6.90	4.12**
Body size (mm)	Bark	4.8 ± 0.83	4.5 ± 0.90	0.75
	Moss	4.0 ± 0.88	4.4 ± 1.00	0.04
	Vine	2.5 ± 0.45	3.3 ± 0.71	0.76
Species richness	Bark	1.5 ± 0.03	1.0 ± 0.04	1.14
	Moss	1.5 ± 0.06	1.5 ± 0.05	0.29
	Vine	1.9 ± 0.05	1.7 ± 0.05	1.07

* $P < 0.02$; ** $P < 0.01$ (all others = $P > 0.17$).

Values are averages ± SE. Paired *t*-tests were used to compare means within substrate types. Bonferroni's $\alpha = 0.025$; d.f. Bark = 16, Moss = 16, Vine = 18.

post-removal, and *Solenopsis* was not more common than *Pheidole* on bare bark baits before vine and moss removal.

Discussion

Central-place foragers can maximise their access to distant resources by choosing pathways that minimise time and energy costs (e.g. Stephens & Krebs, 1986). Cursorial trail-following foragers such as ants accomplish this by investing in the construction and maintenance of persistent paths (as in *Atta* spp.; Howard, 2001) or by adopting pre-existing linear substrates into their foraging network (e.g. Bentley, 1981; Farji-Brener *et al.*, 2007). In the present study we show that the latter strategy facilitates rapid access to patchy food resources in tropical arboreal and semi-arboreal ants. Specifically, ants discovered resources more quickly and accumulated relatively faster on baits associated with vine substrates than moss-covered bark, and these effects disappeared when vines and moss were removed.

The various natural substrates that occur on tropical tree trunks differ radically in terms of physical complexity for an animal the size of an ant. Thus, the observed differences in foraging patterns at baits on vines and moss are not surprising. Vines provide relatively direct, easily navigable, superficially two-dimensional pathways, whereas travelling through moss requires frequent changes in direction and three-dimensional navigation at relatively small spatial scales. This differential effect on ant foraging was evident in our field observations. Specifically, mossy growth on tree trunks presented a substantial barrier to the forward progress of mid-size ants (e.g. *Camponotus* spp.), whereas small ants [e.g. *Solenopsis* (*Diplo.*) spp.] travelled through its interstices and large ants (*Ectatomma ruidum* in this case) walked over its surface with little difficulty. These observations suggest that

differences between moss and vine substrates on tree trunks are analogous to larger-scale differences hypothesised (Kaspari & Weiser, 1999) and observed (Yanoviak & Kaspari, 2000) for ants foraging in arboreal vs. leaf litter settings.

Despite the obvious differences between moss and vine substrates, our prediction of unimodality on the body size distribution of ants foraging on vines was not supported. This is partly due to the methodological constraints of the project. Although some high canopy ants (e.g. *Cephalotes* spp.) will descend to forage at baits placed within 2 m of the ground (Hahn & Wheeler, 2002; this study), our baits were also visited by some large-bodied ground-nesting species (*A. araneoides* and *E. ruidum*) that commonly forage on the understory portions of tree trunks. Had it been feasible to place all baits 1–2 m higher on the tree trunks, we suspect that these taxa would have been replaced by obligate arboreal taxa such as *Azteca* spp., *Crematogaster carinata*, and *Dolichoderus* spp. Given that these taxa occupy the middle range of the body length distribution and show a strong tendency for foraging on vines (S. P. Yanoviak, pers. obs.), their presence presumably would reduce bimodality in the body size frequency distribution, especially on vine substrates.

The difference in average body size among substrates is primarily due to the tendency for several large taxa (*Gnamptogenys*, *Odontomachus*, and *Pachycondyla*) to forage on bare bark surfaces and (to a lesser extent) the presence of tiny *Brachymyrmex* spp. exclusively on vines. Although this implies that vine use is biomechanically or behaviourally biased towards smaller foraging ant species, ongoing studies indicate that this is not the case (C. Silveri, M. Solis and S. Yanoviak, unpublished). Regardless, we suspect that further experimental studies of interactions between body size and vine characteristics (including diameter) are likely to yield interesting community-level patterns, especially if vine diameter mediates interference competition.

The significantly lower ant abundance observed on vine baits post-removal (as shown by paired analysis) was not expected, and suggests that vines provide access to areas on trees that ants might otherwise avoid, perhaps due to light conditions or other factors not measured in this study. Alternatively, if numerically dominant species are frequently using a given vine substrate (e.g. to minimise pheromone trail loss or avoid competitors), the destruction of a commonly used foraging trail may prompt avoidance of the area by those species.

In summary, observations of foraging behaviour (Bentley, 1981, this study) indicate that ants preferentially use vine-like substrates to access distant patchy resources when alternative substrates are present. However, the mechanisms for opportunistic use of vines by foraging ants remain unclear and likely are the product of at least three factors. First, preferential vine use may be an effect of surface rugosity rather than linearity if vines generally offer smoother pathways than other substrates. Second, arboreal ants may forage (or escape attackers) more efficiently on small cylindrical surfaces for biomechanical or sensory reasons; perhaps the linear aspect of vines offers a reliable physical alternative to intensive maintenance of costly chemical trails. Finally, a propensity for vine use could be unrelated to locomotion if ants are using

them as nest sites, or if scout ants are behaviourally conditioned to access extrafloral nectaries and other food resources via certain vines in their foraging territory (Bentley, 1981). Given that lianas and vines are important ecological components of tropical forests, and are generally increasing in abundance (Phillips *et al.*, 2005), understanding links between lianas and ant behaviour and diversity provides a mechanistic framework for predicting the long-term effects of changing forest structure on animal communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Table S1. Repeated-measures ANOVA results for ant-related abundance.

Table S2. Repeated-measures ANOVA results for ant absolute abundance.

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Supplementary Table S1. Results of repeated-measures ANOVA testing differences in ant relative abundance at baits on three substrates (vine, bark, moss) over time. SS = Type III sum of squares, MS = mean square.

Effect	df	SS	MS	F	P
Bait Location	2	1.693	0.846	3.51	0.032
Error	90	20.99	0.241		
Time	6	6.491	1.082	22.99	<0.001
Location*Time	12	1.287	0.107	2.32	0.007
Error(Time)	540	24.98	0.046		

Supplementary Table S2. Results of repeated-measures ANOVA testing differences in absolute abundance of ants at baits on three substrates (vine, bark, moss) over time. SS = Type III sum of squares, MS = mean square.

Effect	df	SS	MS	F	P
Bait Location	2	19.86	9.929	2.28	0.108
Error	90	392.2	4.358		
Time	6	353.9	58.99	73.09	<0.001
Location*Time	12	13.79	1.149	1.42	0.151
Error(Time)	540	435.8	0.807		