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# Surface roughness affects the running speed of tropical canopy ants

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## ABSTRACT

Cursorial central-place foragers like ants are expected to minimize travel costs by choosing the least resistive pathways to food resources. Tropical arboreal and semi-arboreal ants locomote over a variety of plant surfaces, and their choice of pathways is selective. We measured the roughness of tree trunk and liana stem surfaces using laser scanning technology, and explored its consequences for running speed in various ant taxa. The average amplitude of tree trunk surface roughness differed interspecifically, and ranged from 1.4–2.2 mm among three common tree species (*Anacardium excelsum*, *Alseis blackiana*, and *Dipteryx panamensis*). The roughness of liana stems also varied interspecifically (among *Tontelea ovalifolia*, *Bauhinia* sp. and *Paullinia* sp.) and was an order of magnitude lower than tree surface roughness (mean amplitude ranged 0.09–0.19 mm). Field observations of various ant species foraging on tree trunks and liana stems, and on dowels covered with sandpaper, showed that their running speed declined with increasing amplitude of roughness. The effect of roughness on running speed was strongest for mid-sized ants (*Azteca trigona* and *Dolichoderus bispinosus*). The accumulation rate of ants at baits did not vary with tree surface roughness, but was significantly lower on moss-covered versus moss-free bark. Collectively, these results indicate that the quality of plant substrates can influence the foraging patterns of arboreal ants, but likely is more important for resource discovery than for dominance on bare tree surfaces.

*Key words*: behavior; body size; Costa Rica; Formicidae; locomotion; Panama; rugosity.

FORAGING COSTS TIME AND ENERGY (*e.g.,* Stephens & Krebs 1987, Ydenberg *et al.* 1994). For central-place foragers, energetic costs and hazards (*e.g.,* desiccation, predation, disorientation) increase with the distance from the nest to a resource. Cursorial foragers additionally are constrained by their interactions with the three-dimensional characteristics of solid surfaces (Bell *et al.* 1991, Sponberg & Full 2007, Weihmann & Blickhan 2009). Thus, foraging efficiency (*i.e.,* energy gain per unit time) can differ greatly between two equidistant resources accessible by pathways of differing physical complexity. Aside from some experimental studies of ants (*e.g.,* Fewell 1988, Farji-Brener *et al.* 2007), this hypothesis remains largely untested.

Ants and many other small cursorial organisms use plant surfaces as pathways for foraging and as a substrate while feeding. Multiple factors affect the quality of plant surfaces for insect locomotion, and the most conspicuous among these are structural features like roughness or the presence of obstacles (*e.g.,* trichomes, moss, lichens). Analogous to the effects of headwinds and turbulence on volant foragers, such features effectively impose 'drag' on the forward progress of cursorial organisms. Here, we measure this effect using ants running on tree trunks and liana stems as a model system.

Ants are excellent focal organisms for studies of locomotion and foraging behavior; they are abundant and easily observed, they span a broad range of body size, and they are key functional components of most terrestrial ecosystems (*e.g.,* Hölldobler & Wilson 1990, Kaspari & Weiser 1999, Rico-Gray & Oliveira 2007). Although the effects of intrinsic variables (*e.g.,* body size) on ant locomotion have been carefully explored (*e.g.,* Zollikofer 1994a,b, Steck *et al.* 2009), effects of substrate characteristics and other extrinsic factors on ant foraging behaviors are poorly known (*e.g.,* Zollikofer 1994c, Weihmann & Blickhan 2009, Yanoviak *et al.* 2012). The quality of foraging substrates is potentially relevant to larger scale patterns (*i.e.,* local community structure), especially in cases where rapid access to patchy food resources affects competitive interactions. Specifically, in assemblages where dominance-discovery trade-offs exist (Davidson 1998, Adler *et al.* 2007), the persistence of subordinate species likely depends on rapid discovery of unpredictable resources. Thus, understanding habitat-based constraints on foraging behavior can contribute to understanding the mechanisms affecting local diversity in ant communities.

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The choice of foraging pathways should be particularly relevant to the ecology of tropical arboreal ants. The reticulate network of tree branches and plant stems physically limits the number of routes available to a forager, which presumably increases the frequency of interspecific encounters while also constraining them in space. Moreover, our observations in various Neotropical forests show that arboreal ants commonly use lianas (woody vines) to access food resources in different trees (Yanoviak *et al.* 2012, Yanoviak 2015), and ants accumulate at baits relatively faster when they travel over linear pathways such as lianas, than over more complex substrates, such as moss-covered tree trunks (Clay *et al.* 2010). Here, we explore these patterns quantitatively by characterizing substrate roughness using laser scanning technology.

The principal objectives of this project were twofold. First, we quantified the surface roughness (*i.e., microrelief* or *rugosity*) of some common tropical tree trunks and liana stems at scales that are relevant to ants. Second, we measured how surface roughness influences the running speed of foraging ants on experimental and natural substrates. Specifically, we predicted that ant foraging speed would decline linearly with increasing roughness (Fig. 1). Likewise, we expected that ant accumulation rates at baits would be lower on rougher surfaces. Finally, we predicted that these patterns would differ according to body size, such that maximum absolute running speed increases with increasing body size on relatively smooth surfaces.

## METHODS

STUDY SITE.—Fieldwork was conducted in June–August 2008 at the La Selva Biological Station, Costa Rica (10°25′51″ N, 84°00′23″ W), and during the wet season (May–December) of 2013 and 2015 on Barro Colorado Island (BCI), Panama (09°09′15″ N, 79°50′50″ W). Detailed information about these sites is provided elsewhere (McDade *et al.* 1994, Leigh *et al.* 1996). We examined the effects of surface roughness on ant running speed experimentally using wood dowels at La Selva and BCI, and observationally on natural tree trunks and liana stems on BCI. Laboratory-based analyses of stem surfaces were conducted in the Bioimaging Center at the University of Delaware.

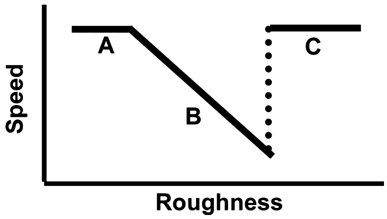

FIGURE 1. Predicted effects of relative substrate roughness (as a proportion of stride length) on ant running speed (also see Steck *et al.* 2009). Ant speed is expected to be constant below a threshold roughness amplitude (A) that is considerably smaller than stride length. As roughness increases relative to stride length, biomechanical efficiency decreases (presumably linearly), resulting in reduced speed (B). Eventually the magnitude of the roughness greatly exceeds stride length and the substrate is perceived as a series of relatively smooth peaks and valleys (C). In this latter phase, the actual distance travelled is greater, and thus apparent speed is reduced, but absolute speed is similar to (A).

TREE TRUNK AND LIANA STEM RUGOSITY.—We used specialized laser scanning equipment (LaserBark; Van Stan *et al.* 2010, Legates *et al.* 2014, Van Stan *et al.* 2016) to quantify the rugosity of 15 individuals of each of three tree species on BCI. LaserBark employs a self-propelled laser scanner mounted on an elevated track that partially or completely encircles a tree trunk (Fig. 2). Data generated by the scanner are compiled in real time to provide a digital profile of a transverse section of the trunk at a given height. Each complete scan reveals the major contours of the trunk, the centroid of its circumference, and the fine-scale rugosity (0.07 mm resolution) of the trunk surface (Fig. S1). These data are subsequently compared against a smooth surface of similar dimensions (*i.e.,* the moving average) to quantify the surface microrelief following standard mechanical engineering guidelines for profile filtering (ASME 1996). Specifically, this process measures rugosity in terms of its amplitude (*i.e.,* height of asperities) and slope (*i.e.,* incline of asperities). Further detail on how the ASME standard is applied to LaserBark data can be found in Van Stan *et al.* (2016).

The focal tree species for this part of the study were *Dipteryx panamensis*, *Alseis blackiana*, and *Anacardium excelsum* (hereafter, referenced by genus only). We chose these species because they are common on BCI and qualitatively span a range of trunk surface rugosity that was expected to be relevant to the locomotion of a typical canopy ant. Tree trunks were scanned at heights ranging between 1.0 and 1.5 m above the ground. Small trees were scanned around their entire circumference, whereas large trees (either >90 cm diameter, or with large buttresses) were

FIGURE 2. The LaserBark apparatus in place around an *Anacardium excelsum* tree trunk in Panama. The inside diameter of the LaserBark track is 100 cm. The small white patch on the tree trunk facing the recording unit is bait for ants.

subsampled by scanning one or more representative sectors of the trunk.

To characterize the surface roughness of liana stems, we collected two samples each of *Bauhinia* spp., *Tontelea ovalifolia*, and *Paullinia* spp. As with the focal tree species, we chose these liana taxa because they are common on BCI and easily recognized. Each liana sample was obtained from a different individual, and consisted of a 2–3 cm length of stem 1.0–1.5 cm in diameter. The stem segments were fixed in 16 percent EM-grade paraformaldehyde diluted to 4 percent in 1 percent phosphate buffer solution.

We used a Zeiss LSM 710 (Carl Zeiss SMT, Oberkochen, Germany) laser scanning confocal microscope to image the liana stem samples using both reflected light and autofluorescence (generated by 561 and 405 nm lasers, respectively). Each liana sample was successively imaged lengthwise along its surface using a 5X/0.25 N.A. objective lens, resulting in up to 18 scans per stem. Data from the scans (a Z-stack of 512 × 512 pixel 12-bit images) were compiled with the Zen 2011 (Carl Zeiss SMT, Oberkochen, Germany) software topography module to generate three-dimensional profiles of the stem surfaces (Fig. S2), which were then analyzed to determine surface roughness. We quantified surface roughness as absolute and average wave amplitude (*i.e.,* peak to valley distances) using both high- and low-pass filters (*i.e.,* high and low resolution) during image processing. A first-order Gaussian fast Fourier transform filtering algorithm was used for both low- and high-pass filtering. Ultimately, we focused on the low-pass data because they rendered a surface that was appropriate for ant-scale features (Fig. S2).

ANT BODY SIZE AND RUNNING SPEED.—We measured the body size of 49 ant species collected from various tree trunks baited with a tuna-honey mixture in Costa Rica and Panama (Table S1). We used a stereoscope fitted with an ocular micrometer to measure the total body length from the anterior margin of the clypeus to the apex of the abdomen (hereafter, BL), thoracic length (*i.e.,* Weber's length [WL]), and midleg and hind leg length (L2 and L3) from the base of the femur to the apex of the tarsus to the nearest 0.01 mm. Relative midleg length ($L2'$) was calculated as L2/WL following Zollikofer (1994b). Only minor workers were measured for dimorphic taxa (*e.g., Pheidole* spp.) and only mid-size workers were measured for polymorphic taxa (*e.g., Azteca* spp.). We measured 1–5 workers for each species and used the median as the datum for analysis. A principal components analysis showed that L3 provided the best overall estimate of body size, and was highly correlated with L2, BL, and WL ($r > 0.96$). Thus, hereafter, we focus on L3 and $L2'$ only.

To explore the effects of interspecific differences in body size on running speed, we measured the time required for 12 common arboreal species (opportunistically selected from the 49 measured as described above) to run 10 cm on *Dipteryx* bark. We limited these trials to *Dipteryx* because it was the smoothest of the three focal tree species. Up to 50 individuals of each ant species were tested (minimum $N = 6$), and running trials were conducted on two or more different *Dipteryx* trunks. For each trial, we selected an epiphyte-free section of the tree that was representative of the trunk surface in terms of roughness. Within that section, we marked the trunk at 10 cm intervals in concentric circles originating from a focal point. An individual ant was then released at the focal point and the time required for it to run 10 cm was recorded with a stopwatch. Only data from uninterrupted, rectilinear runs were used. Air temperature was recorded near the trunk at the start and end of each series of trials.

ROUGHNESS EFFECTS ON ANT SPEED AND ACCUMULATION RATE.—To quantify intra- and interspecific variation in running speed on surfaces of different natural roughness, we measured the time required for workers of four ant species to run 10 cm on trunks and stems of the focal tree and liana species described above. Trunks and stems were marked in 10 cm intervals and between 7 and 30 workers each of *Azteca trigona*, *Dolichoderus bispinosus*, *Crematogaster brasiliensis*, and *Cephalotes atratus* were recorded on each substrate as described above. We chose these ant species because they are common on BCI and represent a broad range of body size. As *Paullinia* and *Bauhinia* stems were quantitatively similar in rugosity (Table 1), we tested ants on one or the other for comparison with the much smoother *Tontelea* stems (Table 1).

To measure accumulation rates of foraging ants on different tree trunks, we baited trees during the LaserBark scanning of tree trunks described above. Tuna-honey baits were placed on each trunk a few cm above the path of the scanner. Each bait was pressed into the trunk furrows over a small area, resulting in a discrete patch *ca.* 3 cm in diameter. When a trunk clearly had a substantial portion of one side covered with epiphytic bryophytes and mosses, we placed one bait on the moss-covered side and one bait on the opposite, moss-free side. In all cases, the mosses were living, but dry (*i.e.,* not covered with water droplets). Bait placement avoided portions of the tree trunk receiving full sun to prevent desiccation. Baits were examined *ca* 5 and 15 min after placement, and every 30 min thereafter for up to 3 h. During each observation, we counted the number of ants of each species present. We recorded all species that visited the baits and did not initially target specific taxa for this part of the study. We also marked the trunk in 10 cm increments along established foraging

TABLE 1. *Quantitative characterization of moss-free trunk surface microrelief for three tree species on Barro Colorado Island.* $N$ = *number of trees measured. Values are means (±95% CI) of root mean squares of the amplitude (mm) and slope (dimensionless) of surface deviations from a smooth form with similar dimensions.* $r$ = *Pearson correlation coefficient for amplitude versus slope* (*$P < 0.05$, **$P < 0.001$). *Within a column, similar letters denote means that do not differ based on* post hoc *Tukey HSD tests. Data were log-transformed before analysis.*

| Species | *N* | Amplitude | Slope | *r* |
|---|---|---|---|---|
| *Alseis blackiana* | 16 | 2.15 (0.470)a | 0.50 (0.152)ab | 0.77** |
| *Anacardium excelsum* | 17 | 1.71 (0.283)ab | 0.66 (0.195)a | 0.74** |
| *Dipteryx panamensis* | 20 | 1.41 (0.296)b | 0.36 (0.108)b | 0.51* |

trails and measured running speed for the four focal species listed above when possible. Bait trials that did not attract ants within 30 min were excluded from the data set. All observations were conducted between 0900 and 1600 h, and we measured air temperature near the bait during each trial.

DOWEL EXPERIMENTS.—We used field and lab experiments to quantify the running speed of ants on substrates of different known rugosity distributed in a relatively regular pattern. We covered four dowels (1 cm diam.) respectively with plain white paper (asperity < 0.05 mm in amplitude) and three different grades of sandpaper having particle sizes of *ca*. 0.1, 0.3, and 1.0 mm in largest dimension (*i.e.,* 320, 120, and 36 grit; Fig. 3). Collectively, these experimental substrates spanned the lower half of the range of roughness observed on trunks and stems (Table 1). Each dowel was marked along its length in 10 cm increments.

We attached the four dowels to a tree at La Selva occupied by *Crematogaster carinata* (one of the most common arboreal ants at this site). The dowels were secured within a few cm of each other and orthogonal to the trunk (Fig. 4), and were left in place for 24 h to allow the ants to acclimate to their presence. We then placed a small amount of tuna-honey bait on the apex of each dowel. After the ants established a foraging trail leading to the bait, we used a stopwatch to measure the time required for one worker to run 10 cm along a dowel from the tree toward the bait. Observations were made sequentially on the four dowels until five ants had been recorded on each. We repeated this five times for each replicate (*i.e.,* 20 observations per replicate; four dowels, five ants observed per dowel) and used the average running speed for the five ants on a given dowel as the datum for analysis. The entire process was replicated 16 times, each on a different tree, and replicate trees were >20 m apart. All data were collected during fair weather between 0800 and 1600 h, and we recorded temperature at the start and end of each replicate.

We duplicated the dowel experiment in the laboratory on BCI (22.2 ± 0.5°C; 81 ± 3% RH) using *C. atratus* as the focal species. We used *C. atratus* in this case because it is easily handled in the lab (and the easiest of the four focal species used in field trials), and it provided an opportunity to compare lab and field results within a taxon. A smooth dowel (roughness < 0.05 mm in amplitude) and three additional dowels covered with sandpaper as described above were suspended between two wooden supports in the lab. We released 30 *C. atratus* workers individually near one end of each dowel and recorded the time required for each ant to traverse a 10 cm section near the center of the dowel. We then collected and weighed each ant to the nearest 0.1 mg. Ants used in this experiment were obtained from multiple colonies and each ant was tested only once.

FIGURE 3. The four experimental substrates used in the field experiment at La Selva. Clockwise from top left: plain paper (control); 320-, 100-, and 36-grit sandpaper. Ants in the image are *Crematogaster carinata* workers (body length = 3.0 mm).

FIGURE 4. The dowel experiment arranged on a tree trunk at La Selva. A similar series of dowels was used for lab experiments in Panama.

ANALYSIS.—We used nested ANOVA models to assess differences in the amplitude and slope of surface roughness among the focal tree species measured on BCI. Tree size (diameter at breast height [dbh]) was nested within tree species to determine if larger individuals of a species have rougher trunk surfaces. We treated size as a categorical variable (small: <60 cm dbh; medium: 60–80 cm dbh; large: >80 cm dbh) for these analyses, because diameters were estimated for trees with large buttresses. We similarly compared the amplitude of liana stem rugosity among species and between samples nested within species.

We used linear regression to assess variation in average running speed of ants on the different roughness amplitudes of the natural and experimental (sandpaper) substrates. Individual ant mass and air temperature were included in the regression model for lab-based and field based trials, respectively. We also used regression to determine how average ant accumulation rate (interpolated as individuals per min) at baits on tree trunks varied with roughness slope and amplitude of tree surfaces. We used Wilcoxon tests to compare the running speed and accumulation rates of ants visiting baits on moss-covered bark and moss-free bark of a given tree type. All data were tested for normality before analysis (with Shapiro–Wilk tests) and log-transformed as necessary to meet test assumptions. All tests were conducted with JMP software v. 8.0 (SAS Institute, Inc., Cary, North Carolina).

## RESULTS

The rugosity of moss-free trunk surfaces differed among the three focal tree species such that *Dipteryx* was smoother than *Alseis* in terms of roughness amplitude and smoother than *Anacardium* in terms of roughness slope (Table 1). The amplitude and slope of roughness of moss-free bark were correlated within each species (Table 1), and average roughness slope and amplitude were similar among tree sizes within a species (nested ANOVA: $F_{6,44} < 2.24$, $P > 0.06$). These quantitative LaserBark results corroborate our qualitative assessment of the trees in the field. Specifically, trunk surfaces of *Dipteryx* appear relatively smooth compared to *Alseis* or *Anacardium* (Table 1). Contrary to our expectations, paired analysis of data from five *Anacardium* trees showed no difference in the slope and amplitude of roughness between bare bark and moss-covered bark ($t < 0.38$, df = 4, $P > 0.72$), which apparently is an artifact of the laser scanning method (see Discussion).

Based on the average amplitude (±95% CI) of roughness, *T. ovalifolia* stems were consistently very smooth (0.09 ± 0.010 mm), and significantly smoother than both *Bauhinia* sp. (0.19 ± 0.033 mm) and *Paullinia* sp. (0.15 ± 0.023 mm), which were similar to each other in terms of roughness ($F_{2,78} = 17.40$, $P < 0.0001$). Collectively, the amplitude of liana stem roughness was 10 times lower than tree trunk roughness (Table 1). Nested analysis and *post hoc* Tukey tests showed significant differences between the two stem sections for *Bauhinia* sp. and *Paullinia* sp., but not for *T. ovalifolia* ($F_{3,78} = 8.98$, $P < 0.0001$). As with the LaserBark results described above, these stem sample results support our observations in the field; specifically, small *T. ovalifolia* stems tend to be very smooth over most of their length relative to other species.

Measurements of 11 common ant species (representing five genera and three subfamilies) on *Dipteryx* trees showed that their absolute speed increases with body size (Fig. 5), and that they are consistently fast, with relative speeds >10 body lengths/s. The relative midleg length (L2′) of these 11 species averaged 2.5 (range = 1.4–3.6; Table S1). Zollikofer (1994b) reported similar L2′ values for workers of 11 species (mean = 2.3, range = 1.6–2.8). The narrower range he observed presumably reflects narrower phylogenetic breadth; 10 of the measured species are in the same subfamily and represent just three genera. Similar to Zollikofer (1994b), the running speed of the 11 species in this study showed no quantitative relationship with L2′ ($F_{1,10} = 0.009$, $R^2 < 0.001$, $P = 0.93$). Although the number of focal taxa in this study was too small to account for phylogenetic effects, there was some conspicuous divergence in running speed among taxa in the middle of the distribution (*i.e.,* L3 = 3–6 mm). Specifically, *Camponotus senex* workers were considerably faster than *Azteca instabilis* and *Cephalotes* spp. workers of comparable size (Fig. 5).

The running speed of three of the four focal ant species (*A. trigona*, *C. atratus*, and *D. bispinosus*) declined with increasing roughness amplitude of natural substrates (Fig. 6). The running speed of *C. brasiliensis* also declined with increasing roughness (Fig. 6), but there was a significant interaction between roughness and air temperature ($F_{1,84} = 38.6$, $P < 0.0001$; *i.e.,* the trials conducted on the smoothest trunks were also inadvertently conducted at warmer temperatures than trials on rougher trunks). The running speed of *A. trigona*, *C. atratus*, and *D. bispinosus* increased minimally with temperature ($F_{1,131} = 4.73$, $R^2 = 0.035$, $P = 0.032$), and there was no interaction between temperature and surface roughness for these three species. The effect of temperature was minimal over the range observed in the field (28–31°C), and removing temperature from the regression model caused only a minor reduction in explanatory power ($R^2$ decreased by <0.04 in all cases).

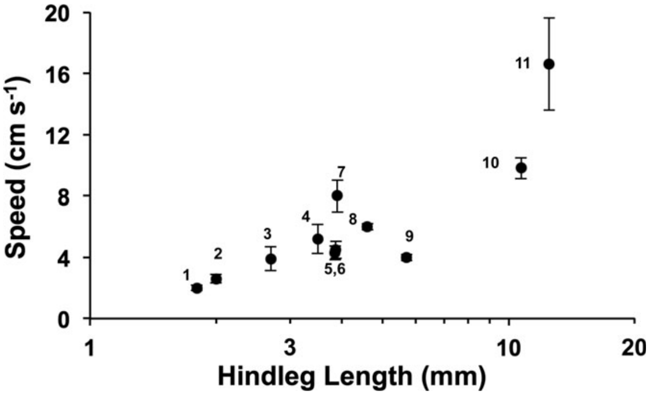

FIGURE 5. Average (±95% CI) running speed of various arboreal ant species versus their hindleg length (L3). All running trials were conducted on *Dipteryx panamensis* trunks at temperatures between 29–31°C. Numbers adjacent to plotted points indicate species as follows: 1 = *Pheidole* nr. *dasypyx*, 2 = *Crematogaster brasiliensis*, 3 = *Pseudomyrmex oculatus*, 4 = *Azteca trigona/chartifex*, 5 = *Cephalotes umbraculatus*, 6 = *Cephalotes basalis*, 7 = *Camponotus senex*, 8 = *Azteca instabilis*, 9 = *Dolichoderus bispinosus*, 10 = *Cephalotes atratus*, 11 = *Neoponera villosa*. L3 was highly correlated with running speed ($r = 0.82$, $P < 0.002$), but we caution that these results do not account for phylogenetic effects.

In the dowel experiment conducted at La Selva, *Crematogaster carinata* running speed declined with increasing substrate roughness ($F_{1,60} = 20.6$, $R^2 = 0.29$, $P < 0.0001$; Fig. 7). There was no statistical interaction between temperature and substrate roughness in this experiment, and running speed increased only marginally with temperature over the observed range ($F_{1,60} = 3.08$, $P = 0.08$). The dowels were occupied almost exclusively by *C. carinata* workers foraging in a column. However, stray workers of *Ectatomma* spp. and *Pseudomyrmex* spp. were occasionally observed foraging alongside *C. carinata*. Workers of *Brachymyrmex* spp. also established foraging trails between the sand grains on the roughest dowels on four separate occasions (three also occupied by *C. carinata*). No aggressive interactions were observed among these taxa.

The running speed of *C. atratus* workers in the lab on BCI was unaffected by the range of experimental roughness provided by the sandpaper, and was similar to the speeds observed in the field. Specifically, *C. atratus* workers ran along the dowels at an

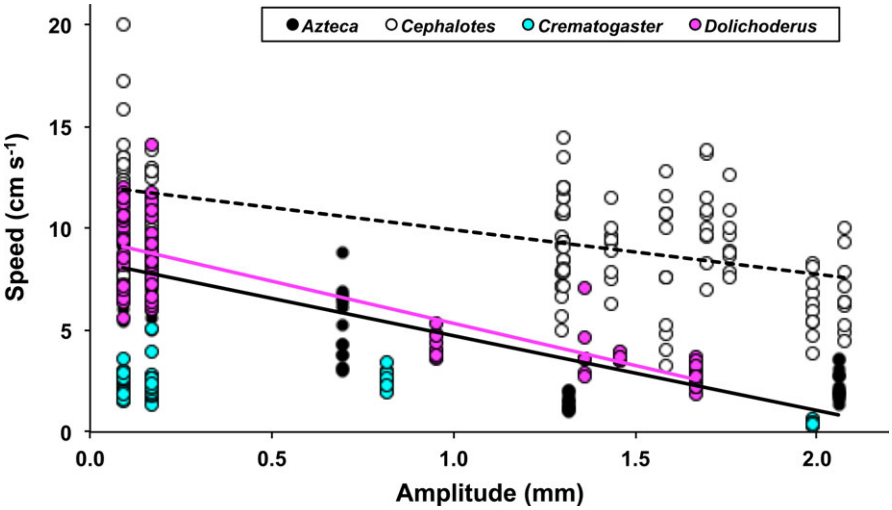

FIGURE 6. Ant running speed as a function of liana stem or tree trunk surface roughness amplitude for four common arboreal ant species on Barro Colorado Island. Results for *Crematogaster brasiliensis* were confounded by temperature differences, but the running speed of the other species declined significantly with increasing roughness (*Cephalotes atratus*: $F_{1,130} = 56.0$, $R^2 = 0.329$, $P < 0.0001$; *Dolichoderus bispinosus*: $F_{1,98} = 234.8$, $R^2 = 0.751$, $P < 0.0001$; *Azteca trigona*: $F_{1,102} = 302.8$, $R^2 = 0.748$, $P < 0.0001$).

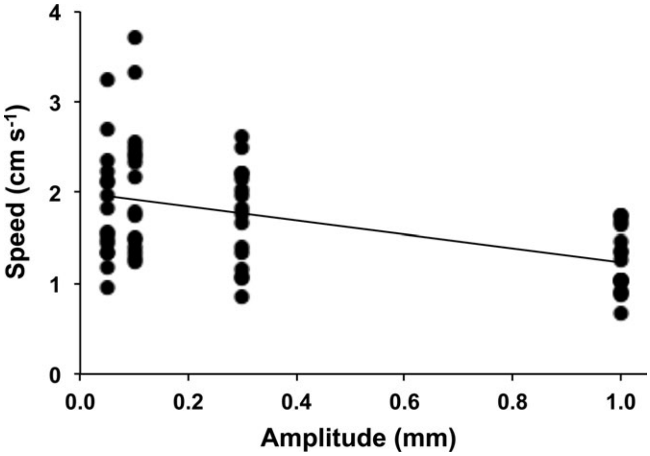

FIGURE 7. Running speed of *C. carinata* workers on 1 cm diameter dowels of differing experimental roughness. Each point is the average of five workers at each roughness amplitude in $N = 16$ replicate trials.

overall average (±SD) 10.0 ± 2.42 cm/s regardless of the roughness amplitude ($F_{1,116} = 1.89$, $P > 0.17$). Larger *C. atratus* workers ran faster than smaller workers ($F_{1,116} = 6.01$, $P = 0.016$), but ant mass explained only a small proportion of the variance in running speed ($R^2 = 0.052$). There was no interaction between ant mass and substrate roughness ($F_{1,116} = 0.83$, $P > 0.36$).

Baits placed on tree trunks to measure ant accumulation rates collectively attracted 15 different species; however, only *D. bispinosus*, *Azteca* spp., and *Ectatomma ruidum* visited at least five baits, which we used as the minimum for analysis. For these three species, the number of workers arriving per min on moss-free bark did not vary with slope or amplitude of surface rugosity ($F < 3.33$, $R^2 < 0.24$, $P > 0.09$ in all tests). *Azteca* spp. clearly avoided baits on moss-covered trunk surfaces, and only *D. bispinosus* and *E. ruidum* were observed foraging on moss-covered bark in sufficient numbers for quantitative comparison with moss-free bark. The larger of these (*E. ruidum*) is a ground-nesting ant that is relatively uncommon on tree trunks at heights >2 m, whereas *D. bispinosus* often nests in treecrowns and will descend to forage at baits in the understory. Although the LaserBark results showed no difference in roughness between moss-covered and bare *Anacardium* bark, foraging *D. bispinosus* workers were eight times slower when moss was present (Wilcoxon $Z = 2.36$, $P < 0.001$). Likewise, *E. ruidum* workers ran twice as fast on bare versus moss-covered *Anacardium* bark ($Z = 3.88$, $P < 0.001$).

In addition to the quantitative results summarized above, we frequently observed *C. senex*, *Cephalotes basalis*, and *Pseudomyrmex oculatus* diverting their foraging trails over rougher, moss-covered surfaces to avoid direct encounters with *A. instabilis* workers. However, these species were never observed actively foraging in moss-covered areas, suggesting that they use the moss as a refuge from interference competition. As observed in other studies (Clay *et al.* 2010), *C. senex* workers in this study commonly used hemiepiphyte roots as highways to avoid moss-covered tree surfaces.

We observed two instances where the differences in ant running speed and accumulation rate at baits on tree trunks ultimately had important consequences for bait occupancy. Specifically, *C. brasiliensis* workers gradually approaching a bait on a bare *Anacardium* trunk were overtaken by workers of *Solenopsis* sp. and *Ectatomma tuberculatum*. The latter species discovered the bait after the *C. brasiliensis* scouts, but were able to steal or defend the bait well before additional *C. brasiliensis* workers arrived. Although *E. ruidum* and *C. brasiliensis* workers appeared to establish foraging trails haphazardly with respect to conspicuous bark features, the much smaller *Solenopsis* workers clearly established foraging trails within the bark furrows.

## DISCUSSION

The hazards of foraging should be especially problematic for arboreal ants, which travel relatively large distances over terrain that is structurally and thermally highly variable (Kaspari *et al.* 2015), and then compete with other ants for access to food patches. Thus, arboreal ants should be under strong selection pressure to choose the most efficient pathways to resources. Indeed, arboreal and semi-arboreal ants will opportunistically incorporate linear substrates into their foraging trails (Farji-Brener *et al.* 2007, Clay *et al.* 2010, Yanoviak *et al.* 2012). It is likely that the micro-roughness of surfaces also affects the choice of foraging pathways. However, until recently, quantification of stem surface properties at scales relevant to ants in the field was difficult or impossible. Here, we measured the surface roughness of tropical tree trunks and liana stems, and showed that stem rugosity affects the locomotor performance of arboreal and semi-arboreal ants.

The 11 arboreal species recorded on *Dipteryx* in this study all were quite fast, and rapid running appears to be relatively common among canopy ants. The reticulate structure of canopy vegetation embedded in a hot, dry environment necessitates mechanisms for escape by quickly traversing relatively long distances. Some species accomplish this by jumping from branches (*e.g.*, in response to alarm pheromones; Yanoviak & Dudley 2006), but most simply run. Moreover, many arboreal species exhibit 'high tempo' behavior fueled with diets rich in carbohydrates derived from phloem-feeding insects (Davidson 1997, Davidson *et al.* 2003). We did not measure running speeds of litter- or soil-dwelling ants for comparison, but we presume that arboreal ants generally are faster than forest floor species. Lab-based results from other studies (Weihmann & Blickhan 2009, Kaspari *et al.* 2016) do not support this conclusion, but additional field data are needed to determine if running speed has a strong habitat component.

In contrast to the honeydew produced by sap-sucking insects, scavengable protein (*e.g.*, dead insects, bird feces) tends to be temporally and spatially unpredictable in the canopy (Yanoviak & Kaspari 2000). Consequently, opportunistic and predatory species—those that rely on rapid discovery or pursuit of resources (Davidson 1998, Adler *et al.* 2007)—should be relatively fast ants. Although testing this hypothesis in the context of the of the dominance-discovery trade-off was not a focus of this study, our qualitative observations of species turnover at baits, and the quantitative comparison of running speed on *Dipteryx* bark, suggest that opportunistic species (*e.g.*, *C. senex*) are faster runners than similar-sized aggressive taxa (*Azteca* spp. and *D. bispinosus*). Likewise, the lack of an effect of surface roughness on accumulation rates of these behaviorally dominant taxa further supports the conclusion that fast running is more important for discovery-based foraging.

The results of the dowel experiments in combination with measurements of four common species on tree trunks show that surface roughness can influence running speed in ants. Overall, these results support the linear reduction in running speed with increasing rugosity predicted in Figure 1. However, running speeds for all species were more resistant to the range of natural variation in tree surface roughness than we expected; ants of all sizes were only conspicuously slowed by the roughest substrates (*e.g.*, *Anacardium* bark and 36 grit sandpaper). The magnitude of this effect appeared to increase with decreasing ant body size, although the field trials for the smallest focal species (*C. brasiliensis*) were inconclusive.

Collectively, the results of this study indicate that ant running speed is very resistant to obstacles that are less than *ca.* 33 percent of body length in amplitude. This pattern likely is a consequence of the stability and efficiency of the alternating tripod gait (*e.g.*, Reinhardt & Blickhan 2014), and is comparable to that observed for cockroaches running on rough experimental terrain (Sponberg & Full 2007). However, identifying a specific threshold of relative obstacle size that causes dynamic instability will require experimentation with a more complete distribution of roughness amplitudes (*i.e.,* filling the gap in our data between 0.4 and 1.0 mm amplitude), and more ant species. Also, we cannot exclude other potentially important effects on running performance, including the vertical inclination or diameter of the test surfaces (Gladun & Gorb 2007, Weihmann & Blickhan 2009), differences related to plant species identity (*e.g.*, the presence of chemical deterrents, cuticular waxes, etc.), and subtle changes in ant gait with speed or in response to surface characteristics (*e.g.*, Reinhardt & Blickhan 2014, Wahl *et al.* 2015).

Running speed partly depends on reliable contact with a substrate, which in ants and other insects is effected via adhesive tarsal pads and claws that function on diverse surfaces (*e.g.*, Orivel *et al.* 2001, Grohmann *et al.* 2015). The effects of surface roughness can be overshadowed by substrate compliance if, for example, softer surfaces enhance the effectiveness of the tarsal claws. We suspect that the relatively soft, spongy bark surface of *Alseis* provides more secure footing than *Anacardium* bark despite its greater roughness amplitude. Likewise, differences in the meso-scale distributional pattern of microrelief (*i.e.,* the ridge-and-valley mosaic typical of furrowed tree bark) affect the rate and consistency with which ants encounter obstacles. This could explain why the running speed of *C. atratus* workers was not affected by coarse sandpaper in the lab but was slower on *Anacardium* in the field despite the similar roughness amplitude of these substrates. Regardless, the biomechanical and physical mechanisms that facilitate ant tarsal adhesion to diverse natural surfaces (*e.g.*, trichomes or waxy coatings; Federle *et al.* 2000, 2002, 2004) deserves further study using substrates that permit experimental manipulation of roughness slope and amplitude independently.

The results of this and related studies (Yanoviak *et al.* 2012) show that ant body size affects their interaction with plant surfaces when foraging. Microrelief of just 2 mm in amplitude can be a significant obstacle for tiny arboreal ants (*e.g.*, *Brachymyrmex* spp., *Solenopsis* spp.), and moss-like growth on tree bark slows the forward progress of mid-sized ants like *Camponotus* spp. and *D. bispinosus* (Clay *et al.* 2010). These patterns generally follow the predictions of the size-grain hypothesis (*i.e.,* that differences in body size among ants shape their interactions with their physical environment; Kaspari & Weiser 1999).

Finally, the LaserBark measuring system provided a portable and efficient method for quantifying the roughness of natural substrates. However, it has two limitations that should be taken into consideration for studies such as this one. First, when used as described here, the scanner only measures circumferential roughness; thus, it does not measure vertical longitudinal furrows that may be relevant to insect locomotion. The ants in this study commonly followed diagonal or circumferential paths on the focal trees, so we do not consider this to be a significant problem. Second, because LaserBark measures changes in the properties of reflected laser light in two dimensions, it did not penetrate porous moss growth on tree surfaces to reveal its three-dimensional physical complexity. Ultimately, understanding the movement patterns of cursorial animals like ants on porous or compliant surfaces requires measurement of adhesive forces and the dimensions of interstices, in addition to surface roughness.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. An example of the trunk profile and rugosity information for an *Alseis blackiana* tree provided by LaserBark.

FIGURE S2. Confocal microscope image of a liana stem (*Paullinia* sp.). The x and y axis units are mm, whereas the z axis is $\mu$m.

TABLE S1. *Morphometrics of selected Neotropical ant species.*

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