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ORIGINAL PAPER

Foraging ants trade off further for faster: use of natural bridges and trunk trail permanency in carpenter ants

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Abstract Trail-making ants lay pheromones on the substrate to define paths between foraging areas and the nest. Combined with the chemistry of these pheromone trails and the physics of evaporation, trail-laying and trail-following behaviours provide ant colonies with the quickest routes to food. In relatively uniform environments, such as that provided in many laboratory studies of trail-making ants, the quickest route is also often the shortest route. Here, we show that carpenter ants (*Camponotus rufipes*), in natural conditions, are able to make use of apparent obstacles in their environment to assist in finding the fastest routes to food. These ants make extensive use of fallen branches, twigs and lianas as bridges to build their trails. These bridges make trails significantly longer than their straight line equivalents across the forest floor, but we estimate that ants spend less than half the time to reach the same point, due to increased carriage speed across the bridges. We also found that these trails, mainly composed of bridges, are maintained for months, so they can be characterized as trunk trails. We suggest that pheromone-based foraging trail networks in field conditions are likely to be structured by a range of potentially complex factors but that even then, speed remains the most important consideration.

Keywords Foraging trail · Trunk trail · Carpenter ant · Optimal foraging

Introduction

In pheromone-based foraging trail networks such as those found in *Camponotus* (Jaffe and Sanchez 1984), *Solenopsis* (Wilson 1962) and the leaf-cutting ants *Atta* (Evison et al. 2008), ants follow a chemical foraging trail laid by nestmates. If food is found at a site, foragers returning to the nest will lay additional pheromone, reinforcing the trail, which is also constantly decaying through evaporation. If the trail from the nest does not lead to food, returning foragers will not reinforce the trail; this will then decay beyond the point that it is attractive to potential ant followers (Wilson 1962). Trails that lead ants more rapidly to a resource will tend to prevail over slower trails because faster trails are reinforced at a greater rate against a background of constant pheromone evaporation (Goss et al. 1989; Beckers et al. 1990). As a result, in relatively uniform environments, faster trails are also likely to be shorter trails.

Many studies have shown that, in addition to selecting the quickest (and often therefore the shortest) route, ant colonies can also optimize foraging by, for example, choosing the best resource (Beckers et al. 1990), maximizing forage return by creating an alternative trail route in crowded situations (Dussutour et al. 2004) or finding the shortest route in complex dynamic situations (Reid et al. 2011). Ants' foraging trails are also influenced by the substrate on which they are laid. Locomotory behaviour (Bernadou and Fourcassié 2008) and the pheromone

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trail decay rate are affected by the substrate coarseness (Jeanson et al. 2003). However, a question that has received less attention concerns how ants adapt to differences in the terrain over which they travel. Furthermore, pheromone studies have mostly been carried out in the laboratory under relatively uniform conditions and are therefore limited with respect to the insight they can offer to ant foraging under real and complex ecological scenarios, which will likely include heterogeneous terrain.

One of the few studies that has examined trail optimization under field conditions showed that the wood ant *Formica aquilonia* optimizes the total length of its trail and the distance between the source and nest (Bulh et al. 2009). Ants that forage on the forest floor, like *F. aquilonia*, have a complex three-dimensional foraging environment with fallen branches, trees and roots forming both obstacles and potential walkways. Such opportunist walkways may be useful to ants: trails of the leaf-cutting ant *Atta cephalotes*, for example, were composed of ca. 30 % fallen branches in one site, and foragers walked faster on the fallen branches than on soil (Farji-Brener et al. 2007), even after taking into account the fact that they walked more slowly when ascending and descending the fallen branches (Mongollo and Farji-Brener 2009). So, whilst branches are extremely unlikely to be aligned with the shortest distance to the destination, they may nonetheless provide the quickest route by allowing for faster walking speeds. Branches and other potential walkways are, therefore, an important but common complication of foraging trails. They can be considered analogous to road networks where the quality of the road surface—dirt tracks versus asphalt, for example—can be an important factor in deciding the best route.

Here, we investigate how ants use bridges in a field setting. In particular, we investigate whether ants are able to make use of bridges that are not the most direct route between the colony and the resource but could provide a faster route through increased speed. Preliminary observations showed that the foraging trails of carpenter ants (*Camponotus rufipes*; Hymenoptera: Camponitini) followed fallen branches, twigs and lianas, using these bridges as part of the trail. As this seems to make their trails longer, we hypothesized that the longer route, where it includes these bridges, is the optimal route; that is, the ants are trading off "further" for "faster". If this is the case, then we expect to see a consistency in the pattern of use of these bridges through time, as is seen in leaf-cutting ant trunk trails (Hölldobler and Wilson 1990); thus, we also examined the permanence of the trails of *C. rufipes*.

Methods

Study area and species

Fieldwork was carried out from December 2010 to April 2011 at the *Mata do Paraíso* research station of the Federal University of Viçosa, Minas Gerais, southeastern Brazil (20°48′08 S, 42°51′31 W). This is a recovered fragment of Atlantic rainforest (it was previously a coffee plantation) where the dominant vegetation is a secondary seasonal semi-deciduous montane forest (Veloso et al. 1991). It is characterized by a robust understory, but foliage is not thick at ground level. The ground is typically covered with 10–20 cm of leaf litter. Although there are patches where soil is exposed, this work was carried out in an area where the soil was completely covered by litter. *C. rufipes* is very abundant in this fragment, feeding on nectar and honeydew as well as live arthropods (Jaffe and Sanchez 1984; Del-Claro and Oliveira 2000). In this habitat, *C. rufipes* is active at night, with activity peaking in the early evening (Online Resource 1).

Preliminary observations of the ants revealed that they were making extensive use of fallen branches, twigs, lianas and exposed roots as part of their trails, only rarely walking directly on the forest floor. These "bridges" (parts of the trail not directly on the forest floor) consisted of fallen sticks (branches, barks), exposed roots and lianas and are defined here as having a diameter ≥2 cm and an elevation from the forest floor of ≥2 cm. At some points, the trail also had sections where ants walked directly on the forest floor. The forest floor is here defined as non-woody material (leaves, flowers, seeds that make up the leaf litter) and small woody material (branches, bark<2 cm) resting on the ground or the surface of the litter.

Data collection

Four established nests of *C. rufipes* were identified. These were approximately 1–2 m in diameter and were built on the forest floor up against living trees. The nest is a semi-spherical structure, consisting of small dried leaves and thin twigs (Jaffe and Sanchez 1984). A square plot (10 m×10 m) was demarcated around each nest, such that the nest entrance was at the center. Each plot was sub-divided into a 25-square grid (with each sub-grid square being 2 m×2 m). Foraging trails were identified by the passage of ants along them (see below) and were marked with small flags placed every 30 cm. The trails were marked from the nest entrance until they left the plot. This was done shortly after dusk, when foraging peaked (Online Resource 1) and the trails were clearly defined by the passage of ants. Differently coloured flags were used to identify those parts of the trail following bridges and those occurring on the forest floor (definitions above) (Fig. 1a–c). The coordinates of each flag inside the plot were determined by measuring the x and y distance from an origin defined permanently but arbitrarily as one corner of the 100-m^2 grid (Fig. 1b). The trails were flagged and monitored in this manner once a month for 4 months (December 14, January 12, February 15 and March 15). All the colonies were monitored during the same night. The average size of the ants found on trails was 7.66 mm, being compatible with that of Jaffé and Sánchez (1984) who found that 60–80 % of the ants on trails are medium size (7.7 to 9.9 mm). We searched for ants walking off the trails, but we could not find them within the areas of study.

Temperature plays a role in the walking speed of ants (Jayatilaka et al. 2011). To ensure that any differences in walking speed could be attributed to differences in substrate rather than substrate-related differences in temperature, we measured the temperature at four randomly selected bridges and the forest floor 30 cm north of each bridge point. No experimental manipulation was done because a long-term study was being carried on those areas, where the spatial structure was an important component. Except where otherwise stated, analyses were conducted using R (version 2.12.0).

Do ants use bridges more than the forest floor?

To test whether ants used bridges more than the forest floor for their trails, we calculated the number of bridge flags and soil flags for each trail for each monitoring event and compared them using a generalized mixed model. The mixed model was used to avoid temporal pseudo-replication, using "month" as a repeated factor, since this factor was not independent. The plots were entered first as co-factor. Model simplification was carried out to determine the significance of each variable (Crawley 2007). The initial complete model had month, plots and substrate (bridge or forest floor) as explanatory variables and numbers of flags as the response variable. As the plots were not significant, they were entered as replicates ($\chi^2_3=7.5256$, $P=0.06$).

Do ants trade off "further" for "faster"?

We hypothesized that the ants trade off "further" for "faster" on their trails. To test this, we did two different analyses. Firstly, to see if they are walking further than strictly necessary, we compared the total trail length from nest entrance to plot edge with the theoretical minimal possible distance they could walk to arrive at the same point. The minimal possible distance was calculated trigonometrically. The actual trail distance was calculated by multiplying the number of flags on the trail by 30 cm (the distance between flags). Over the 4 months of study, and in the four plots, we recorded in this manner 20 newly formed trails that led from nest to plot edge (i.e. any trail that was recorded in consecutive months was used only once in this analysis). Here, then, our repetitions are trails rather than plots, independent of the month in which they were recorded. Each actual trail distance was compared with the corresponding minimal theoretical distance, using a paired *t* test.

To test the hypothesis that ants walk faster on bridges than on the forest floor, we compared the speeds of ants walking on each substrate. To record speed, trails were filmed between 7.30 and 8.30 p.m. (when the ants were most active; Online Resource 1) on March 23. Filming was done with a handheld microscope (ProScope HR—Bodelin Technologies, Lake Oswego) at a magnification of ×10 and a distance of 15 cm from the trails (Online Resource 2, 3). This was attached to a notebook computer, and films were recorded as .avi files. The videos were recorded in complete darkness, illuminated by red light (a handheld torch—ShyLux Km-8305—covered with red electrical isolation tape). Due to logistical constraints, two such recordings were taken from three of the plots (and not all four plots), one recording on bridges and one on the forest floor, giving a total of six films. Each recording was 5 min, but as it was necessary to touch the trail with a rule to standardize the camera distance, the first minute of each recording was excluded from all analyses to allow ants to recover from the disturbance. Speed was measured using Observer® XT software (Noldus, www.noldus.com). This plays video recordings in slow motion, and users can record behaviours and duration by pressing specific key sequences. For the first 20 ants that appeared on the screen, for each video, the speeds were recorded. In total, 60 ants for bridges and 54 for forest floor were analyzed (in one colony, only 14 ants were recorded in the 4 min of observation). The speeds were analyzed with a two-way ANOVA via general linear models (GLM). The response variable was speed (cm s^{-1}), with a gamma distribution to account for non-homogeneous distribution (Crawley 2007). The explanatory variables were trail substrate (bridge vs. forest floor) and the colony of origin of the ants. Individual ants were considered replicates.

We also estimated the total time spent using each trail, consisting of bridges and forest floor, and compared it with a hypothetical trail that ran in a straight line only on the forest floor. To obtain the first value, we added (a) the quotient of the length of the trail on the bridge and the mean speed of ants from that colony on bridges (see above) to (b) the quotient of the length of trail on the forest floor and the mean speed on that substrate (t=(distance walked on bridge/speed on bridge)+(distance walked on forest floor/speed on forest floor)). Estimates for the direct route were taken using the direct distance to the edge divided by speed on the forest floor (t=direct distance/speed on forest floor), for each colony. These paired values were compared with a one-tailed paired *t* test.

Do the ants use trunk trails?

Trunk trails are pheromone-marked paths that persist for long period (Hölldobler and Wilson 1990). To test if *C. rufipes* uses trunk trails, we measured the permanence of the trail through time by calculating the Jaccard index (a similarity index). This index is used to compare the diversity and similarity in samples, and it is commonly used in ant species composition studies, comparing the presence/absence of species in different situations (Zelikova and Breed 2008; Gotelli et al. 2011). In our case, each point, represented by numbered flags, was considered one part of the sample set. We calculated the index using the flags placed in the first month as a reference to compare with the following months. Thus, we determined whether each flag present in December was present or absent in each of the subsequent 3 months. The software PAST (version 1.82b) was used to obtain the Jaccard index. The indices were analyzed by ANCOVA via GLM. The similarity index was used as the response variable, using a binomial distribution. The model had time (in days) as an explanatory variable, while nests were used as replicates.

Results

Ants use bridges more than the forest floor

We used a total of 459 flags to follow a length of 1,377 m of newly formed trails during this study. From the total of 459 flags, 394 were on bridges and 65 on the forest floor. This means that, from the length of all trails combined, 92 % was bridges and only 8 % was laid direct on the forest floor. We found 22±5.31 (mean±SE) flags on bridges and 2±0.91 (mean±SE) flags on forest floor per trail. None of the 20 trails followed in this study were completely on the forest floor, but six trails were completely built on bridges. Thus, the majority of the ants' trails followed natural bridges rather than the forest floor (GLM mixed model: $\chi^2_1=71.68$, $P<0.001$) (Fig. 1c), and this remained unchanged through time (GLM mixed model: $\chi^2_3=0$, $P=1$).

For forager ants, a possible negative consequence of following bridges is the time spent climbing on and off the linking sections. An important aspect of the system we observed is that the bridges followed by the ants were often uninterrupted for long distances (several metres). In most case where bridge pathways had more than one twig, liana or root as components, they were either connected at the same level or one section was resting on the other, removing the need to climb on to and off each bridge section.

While there was a statistically significant difference for temperature on bridge (20.563 °C±0.019 (mean±SE)) versus forest floor (20.645 °C±0.104 (mean±SE)) ($t=3.6145$, $df=10$, $P<0.005$), the difference was only 0.081 °C. Ants forage in a temperature envelope that ranges over, at least, 15° (Hölldobler and Wilson 1990; Cerdá et al. 1998; Yamamoto and Del-Claro 2008); therefore, the difference we found cannot be considered to be biologically significant.

Ants trade off "further" for "faster"

Although ants seem to exhibit a preference for walking on bridges, this means they walk further than necessary when real trail length (692.9±152.7 cm (mean±SD), $N=20$) was compared with the hypothetical shortest possible trail length (564.5±67.16 cm (mean±SD), $N=20$) (t test: $t_{19}=3.774$, $P<0.001$).

The speeds of the workers were influenced by the substrate used (bridge or forest floor) (GLM with gamma distribution: $\chi^2_{113}=38.37$, $P<0.001$). The nest of origin also influenced speed (GLM with gamma distribution: $\chi^2_{113}=69.30$, $P<0.001$), and there was an interaction between these two variables (GLM with gamma distribution: $\chi^2_{113}=31.46$, $P<0.001$). Because of the effect of nest and the interaction, we conducted further analyses to determine if the principal result (the effect of bridge on speed) varied with nest of origin, grouping the nest origin (colony A, B or C) and substrate (bridge or forest floor). In this new analysis, our explanatory variables were "trail path+nest" (bridge colony A, forest floor colony A; bridge colony B, forest floor colony B; and so on). We found that the direction of the result was maintained and the nest of origin only affected the strength of the difference in speed (Fig. 2a, Table 1). Using these speeds in conjunction with the lengths of trail found on bridges or on the forest floor,

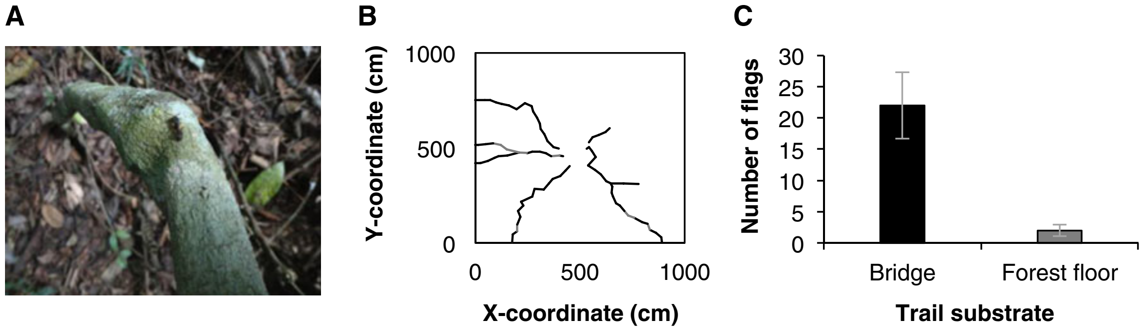

Fig. 1 Use of bridges on foraging trails of *C. rufipes*. **a** Trail marking on bridge substrate (a fallen branch). **b** Representative map of a *C. rufipes* trail (in colony A, December 2010). The *black lines* represent the parts of trail built over bridges and the *gray lines* represent the parts of the trail built directly on the forest floor. **c** Mean (±SE) numbers of flags used to follow trails of the carpenter ant *C. rufipes* on bridges and the forest floor, within an area of 100 m^2 centered on the nest entrance across 4 months of monitoring ($N=4$ colonies)

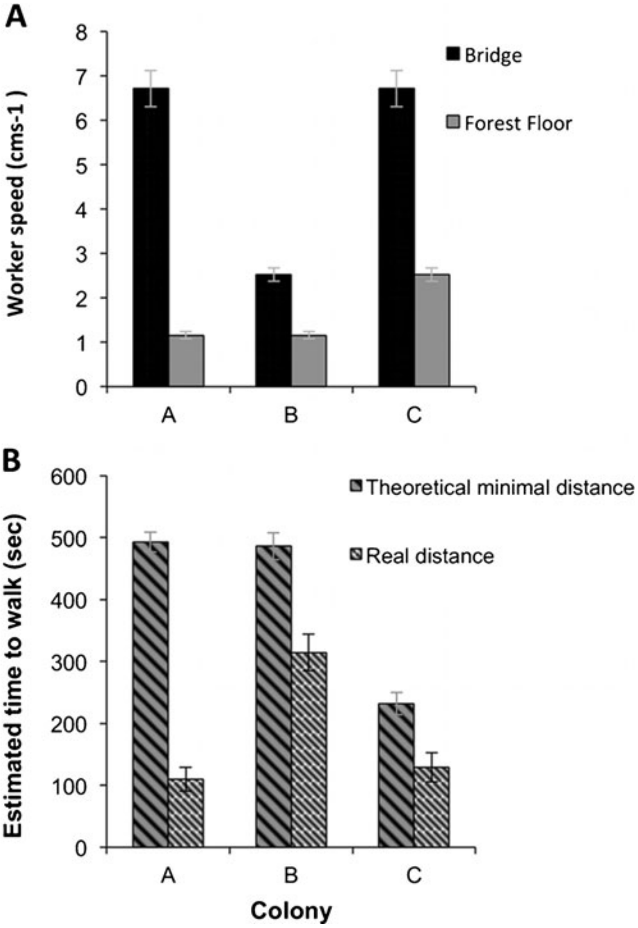

Fig. 2 Trail optimization using bridges of three different nests—A, B and C—of *C. rufipes*. **a** Mean (±SE) worker speeds (cm s^{-1}) on bridges and on the forest floor ($N=60$ ants walking on bridges; $N=54$ ants walking on forest floor). **b** Mean (±SE) estimated times to walk the trail using the theoretical minimum distance through the forest floor versus the real distance ants walked on trails incorporating bridges ($N=19$ trails of three different nests of *C. rufipes*)

we estimate that the ants reached the edges of the plots 2.4 times faster than if they had walked the direct minimal route on the forest floor (Fig. 2b) ($t_{18}=-7.516$, $P<0.001$).

Use of trunk trails

As expected, trail decay is time dependent (GLM with binomial distribution: $F_{[1,31]}=12.956$, $P<0.001$). Trails persisted for considerable periods: approximately 50 % of the trail was maintained after 60 days and 20 % after 80 days (Fig. 3).

Discussion

Our results clearly showed that ant *C. rufipes* makes extensive use of bridges (fallen branches, twigs and lianas) on its trail networks and uses these bridges in preference to the forest floor. Although we did not measure the total availability of bridges on the forest floor and we did not run a preference experiment, the fact that 92 % of trails were bridges argues against the suggestion that ants are randomly choosing bridge substrates based on their availability on the forest floor. According to Schessl et al. (2008), branches >2-cm diameter and large pieces of bark represent only of 7.14 % of litter in Atlantic rainforest. Moreover, the leaves and the small wood (<2-cm diameter), the principal components of the forest floor substrate, make up the largest proportion of litter (69.9 and 23.6 %, respectively). The forest in this study was representative of Atlantic rainforest, and casual observation suggests that these proportions are broadly applicable here. There was certainly no reason to expect the proportion of bridges to be larger than, or even equivalent to, the forest floor substrate.

Studies of ant foraging on pheromone trails typically show that ant trails follow the quickest route, which is also the shortest route in many cases (Jackson et al. 2004; Vittori et al. 2006; Garnier et al. 2009; Reid et al. 2011), and this has inspired computational models and network algorithms (e.g. Ant Colony Optimization) (Lee 2009; Zhao et al. 2010). Here, we have strong evidence that in natural conditions the optimal trail is not usually the shortest but that ants can make use of the complexity of their environment to provide for quicker routes through the selection of trail substrates that increase walking speed. Although they walk 1.22 times further using bridges than they would using a direct route across the forest floor, they walk 3.5 times faster on the relatively unimpeded bridges than they can manage on the complex forest floor. We estimate that overall this means they spend 2.4 times less time walking along the trails they make, which are composed of bridges and forest floor, rather than an ideal straight line trail.

Ants following fallen branches, twigs and lianas have been reported in previous work. For example, it has been noted that *Camponotus sericeiventris* uses branches and lianas as part of their trails, but no additional information is provided

Table 1 Speed of *C. rufipes* workers—from three colonies (A, B and C)—walking on forage trails composed of two distinct substrates: forest floor and bridges

Colony	Worker speed (mean±SD cm/s)	
	Bridge	Forest floor
A	7.022±3.079 a	0.981±0.524 c
B	2.478±0.9249 b	1.277±0.617 c
C	6.412±3.200 a	2.558±1.373 b

The speed is affected by the interaction between colony and substrate. Although the colony has an effect, the direction of the results is the same in all cases: the ants walk faster on bridges than on the forest floor. We compared the speeds by model simplification. Same lowercase letters denote no statistical difference among the means. The statistical significance was $P<0.001$ for all positive comparison

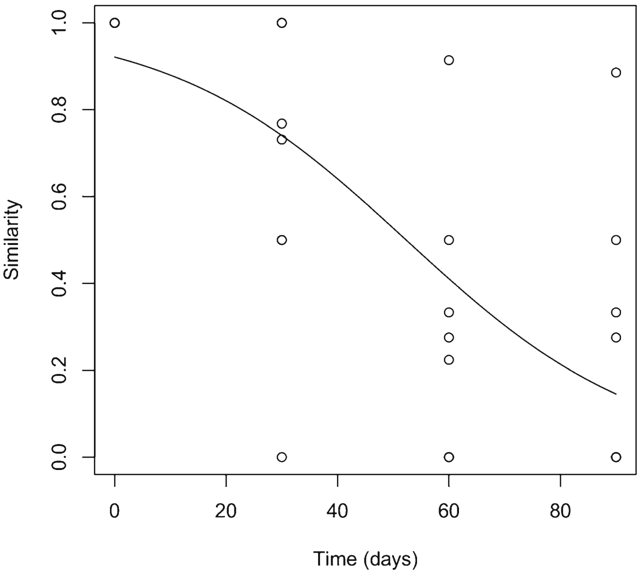

Fig. 3 Foraging trail permanency through time of carpenter ants. The Jaccard index of similarity was calculated for four colonies of *C. rufipes*, relating the trail of December 2010 with the next 3 months (January to March 2011). The similarity indices were analyzed in a logistic regression. Approximately 50 % of trail was maintained after 60 days, and 20 % was maintained in the last observation

(Yamamoto and Del-Claro 2008). Further, 30 % of foraging trails laid by the leaf-cutting ant *A. cephalotes* were found to be objects which we classify as bridges (Farji-Brener et al. 2007), and it was concluded that this may increase speed, even with the time spent climbing on to and off the fallen branches (Mogollon and Farji-Brener 2009). The carpenter ant studied here has 89 % of its trail on bridges, and the bridges are often uninterrupted; thus, we do not expect the ants to spend much time climbing on and off bridges.

We suggest that using bridges has advantages in addition to increasing speed. The total area of the ground that ants contact may be reduced (Online Resource 2). Walking over clear bridges requires only that ants contact the trail with their tarsi, whereas more "untidy" substrates on the forest floor are likely to force contact across more of the ants' cuticles. This may be important in the study area, as the entomopathogenic fungus *Ophiocordyceps camponoti-rufipedis* is commonly found (Andersen et al. 2012). This parasitic fungus controls the behaviour of the infected ant host, leading it to climb to a specific height and bite the lower surface of a leaf. The fungus grows out from the dead ant and shoots spores towards the ground, where new ants can be infected (Andersen et al. 2009). Using bridges reduces potential contact between ants and spores and could thereby reduce the probability of infection, acting as a behavioural defence against parasites (Elliot and Hart 2010). The same thought can be applied to sit-and-wait predators, such as spiders, that inhabit the forest floor. Similarly, ants walking on cleaner substrates will need to invest less effort in grooming.

A further advantage of using lianas, fallen branches and twigs as part of the trail may stem from the use of pheromones to mark the trail. The pheromone trail of the ant *Monomorium pharaonis*, for example, decays more quickly on a newspaper substrate (i.e. a rough surface with absorbent proprieties) than on a plastic substrate (smooth and non-absorbent) (Jeanson et al. 2003). Litter on the forest floor is likely to be a more absorbent surface than bark-covered branches and twigs, so the pheromone trail of *C. rufipes* may evaporate more slowly on bridges. Such differences in surface properties could lead to considerable savings in pheromone production for colonies using bridges, perhaps helping to counter the costs of maintaining a longer pheromone trail.

Besides showing the advantage of using bridges, we provide the first evidence of permanence of a *Camponotus* trail network through an extended period of time in natural conditions. Previous studies have generally focused on daily rhythms (Vasconcellos 1990; Santos and Del-Claro 2009). We have also used a novel application of the similarity index to show that *C. rufipes* maintain 50 % of their foraging trail after 60 days. It is know that ants maintain physical trails by clearing them, as found in other ant groups such as leaf-cutter ants (Vasconcellos 1990) and harvester ants (Azcarate and Peco et al. 2003), which are used for long times, characterizing "trunk trails" (Hölldobler and Wilson 1990). Trunk trails begin on the nest entrance as a thick pathway that bifurcates, leading the ants rapidly and efficiently to the source site (Hölldobler and Wilson 1990). We found no evidence in the literature or in our own observations that carpenter ants maintain these, but now we know that they can use bridges as "highways" for a considerable period of time, allowing such bridges to be characterized as trunk trails.

To conclude, we have shown that the carpenter ant *C. rufipes* uses *objets trouvés*, for example, fallen branches, twigs and lianas, as bridges to structure their foraging trails. These bridges are distributed haphazardly in space and are very unlikely to represent the shortest route. Nevertheless, 92 % of the ants' foraging trail is composed of bridges. We have also shown that using bridges, the ants can walk faster than they would walk directly on the forest floor. We suggest that pheromone-based foraging trail networks in field conditions are likely to be structured by a range of potentially complex factors but that even then, speed remains the most important consideration.

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