Behavioral Ecology

The official journal of the ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2016), 27(4), 1017–1024. doi:10.1093/beheco/arw007

Original Article

Gone with the wind: short- and long-term responses of leaf-cutting ants to the negative effect of wind on their foraging activity

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Received 30 July 2015; revised 30 December 2015; accepted 5 January 2016; Advance Access publication 31 January 2016.

The fitness and survival of organisms ultimately depend on their feeding. Therefore, foraging behaviors should be selected to maximize cost-benefit ratio. Wind may restrict and modify animal movements increasing the cost of foraging, especially when the animal carries resources that intercept wind. We quantified the effect of wind on the foraging of leaf-cutting ants and evaluated whether this effect varies with 1) leaf fragment traits, such as area, mass, and shape, and 2) the characteristics of the foraging trail system. We also tested whether these ants show a short-term response to wind by selecting loads with characteristics that reduce wind interception, and a long-term response, by arranging the spatial design of the trail system in a way that reduces that effect. We found that in windy conditions, the speed of loaded ants was reduced by 55%, and ants were blown off the trail 28 times more than in windless conditions. However, wind only affected ants walking along trails that were perpendicular to wind direction or parallel upwind. Wind effect increased with area, mass, and shape of loads. At the short term, ants reduced the negative effect of wind by selecting smaller, lighter, or more elongated loads. However, trails showed no particular spatial distribution in relation to wind direction. This is the first study that quantifies the negative consequences of wind on leaf-cutting ants' foraging and reports behaviors that can reduce this effect. Our work illustrates how short-term behavioral responses can mitigate the negative effect of an understudied environmental factor on ant foraging.

Key words: **abiotic factors, *Acromyrmex*, forage, resource selection, speed, trail system.**

INTRODUCTION

The fitness and survival of organisms ultimately depend on their feeding. It is known that food quality and quantity affect total egg production, number of offspring, growth rate (Brett 1993; Kant et al. 2012; Pajk et al. 2012), and sexual selection (Davies et al. 2012). Therefore, foraging behaviors should be selected to maximize benefits and reduce costs. Biotic and abiotic factors may influence the cost-benefit ratio of foraging behaviors. The most studied biotic factors are predation risk and competition, which can reduce foraging rate and limit access to food, respectively (Milinski and Heller 1978; Tran et al. 2014). Among abiotic factors the effect of temperature on foraging behavior is widely known, influencing activity periods, the type of behavior (risk averse and risk prone), or decreasing walking speed and foraging success (Avery and Krebs 1984; Caraco et al. 1990; Jayatilaka et al. 2011). Another abiotic factor that may affect foraging is wind, whose effects have been mostly studied on flying organisms (Furness and Bryant 1996; Gilchrist et al. 1998; Weimerskirch et al. 2012). However, the effect of wind on foraging of walking organisms is far-less studied.

The wind may affect the behavior of walking organisms just as it affects flying organisms. For example, in windy conditions, cockroaches change their walking direction (Willis and Avondet 2005); red deer use lower-quality foraging patches (Conradt et al. 2000); and spiders modify the size, structure, and orientation of their webs (Hieber 1984). In ants, the effect of wind on behavior is notorious; wind gusts reduce ant speed and can even blow ants off the foraging trail (Rudolph and Loudon 1986; Anderson and Jadin 2001; Supplementary MOV. S1). For example, in windy conditions, desert ants wander some distance downwind of the food source, and when they detect the odor stream emanating from the food, they change direction and walk upwind on a slightly zigzag path until they reach the food (Wolf and Wehner 2000, 2005). Although other studies have determined how the wind affects ant movements, only one study quantified the effect of wind on ant foraging activity.

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However, their results were nonconclusive because they studied the effect of wind on an ant species that forages in tunnels below ground (Porter and Tschinkel 1987). If wind can decrease food delivery rate to the colony as it hinders ant movements, we expect ants to show behaviors that reduce the negative effect of wind.

Leaf-cutting ants are good models for analyzing the effect of wind on foraging behavior. First, workers cut and collect plant fragments to use them as substrate to cultivate a mutualistic fungus, the source of food for the larvae. Typically, workers carry plant fragments that are several times larger than their bodies. Therefore, these loads greatly increase the area of wind interception potentially affecting movement, walking direction, and speed of loaded ants. Second, ants adjust the area, mass, and shape of their loads depending on the context (e.g., Roces 1994; Lewis et al. 2008; Norton et al. 2013); thus, they may be able to decrease the wind interception surface of their loads. Finally, leaf-cutting ants travel along a system of foraging trails that they maintain clear of vegetation. Foraging trails vary in the spatial orientation and location (Kost et al. 2005), which could also modify the level of wind exposition of the ants walking along them. In sum, leaf-cutting ants allow a useful quantification of the potential consequences of wind on foraging and the behaviors that may reduce these effects.

In this work, we 1) quantified the effect of wind on the foraging activity of leaf-cutting ants and determined whether ants show 2) a short-term response by selecting loads that minimize wind interception and 3) a long-term response by designing permanent trunk-trail system that reduce the potential negative effect of wind. Considering that 1) wind interception increases with load area, 2) the energy that ants need to maintain the load in the adequate position increases with load mass, and 3) the torque, that is, the twisting effect of a force applied to a rotating object, increases with the height of the load (Supplementary Figure S1), we expected that in windy conditions ants select smaller, lighter, and more elongated loads. Regarding the long-term response, because ants carry their loads almost parallel in relation to the main axis of the trail (see Figure 1; Röschard and Roces 2002), we expected that in windy regions trails will not be oriented perpendicular to the prevailing wind direction and that in windless regions trails will be oriented randomly.

METHODS

To evaluate the effect of wind on ant foraging and how ants reduce this potential negative effect, we worked with *Acromyrmex lobicornis* because it 1) cuts monocotyledonous and dicotyledonous species (Fowler and Robinson 1979), and thus, it may select loads with a wide range of characteristics; 2) inhabits open environments (Farji-Brener and Ruggiero 1994) where it is easy to follow workers and perform experiments; and 3) has a wide geographic distribution, inhabiting regions with strong winds mostly from one direction as well as windless regions (Farji-Brener and Ruggiero 1994), which allows us to compare the spatial design of the trail system in windy and windless regions.

Fieldwork was carried out in 2 sites with contrasting wind intensity located in Argentina. The windy site was El Chocón, Neuquén (39°16′S, 68°47′W), characterized by strong winds prevailing from the southwest (speed mean ± standard error [SE]: 20 ± 0.2 km/h, maximum speed: 56 km/h; main direction: 236°; data source Autoridad Interjurisdiccional de Cuencas). The windless site was La Florida, San Luis (33°07′S, 66°03′W), which has significantly lower wind intensity ($t = 76$, $P < 0.001$; speed mean ± SE: 6 ± 0.1 km/h, data source Universidad Nacional de La Punta). The speed means showed are measured at 10 m above the ground, but at ground level, the wind intensity is lower. In the windy site at ground level, the mean speed of wind is 2.5 ± 1.6 km/h (± SE) with gusts of 20 km/h; and during the activity period of *A. lobicornis* (October–May), the windiest month is December, whose mean is 4.4 ± 1.7 km/h (± SE). We conducted the study during Austral spring–summer in 2013–2015. In all field measurements and experiments, we recorded the following wind parameters: the most frequent speed, maximum speed, and direction at ground level. To characterize days and moments as windy or windless, we measured wind speed placing an anemometer perpendicular to the wind in an area without vegetation; to measure the wind speed sensed by ants, we placed it in the same direction of the trail at 1 cm above ground.

To evaluate whether the wind affects the *A. lobicornis* foraging, we carried out comparative and experimental studies. We first evaluated the natural wind effect by filming foraging trails from 19 nests during 150 s in windy and windless days (4–9 and 0 km/h, respectively). To assess whether the effect of wind varies with trail orientation and vegetation around trails (which might work like a wind barrier), we filmed loaded ants along trails parallel and perpendicular to the wind direction (180 ± 20° and 90 ± 20°, respectively), and with/without surrounding vegetation that potentially act as "windbreaks." We measured ant speed and the proportion of ants that were blown off the trail. To estimate ant speed, we selected 10 ants of 4–5 mm of length per video (the most abundant ant size in the foraging trails; Alma AM, personal observation) and measured the time spent by each ant to walk 10 cm of trail. Considering that fragment size affects ant running speed (Bollazzi and Roces 2011), we chose ants whose loads were similar in size. We only considered ants that were not blown off the trail for ant speed estimation. To calculate the proportion of ants that were blown off the trail per nest, the number of ants that were blown off at least once was divided by the total number of ants that were video recorded. Ant speed was log-transformed to meet analysis assumptions and analyzed using linear mixed-effect models. For each model, wind condition, trail orientation, and vegetation presence were considered as fixed factors and nest identity as random factor. We tested whether the random effect was significant using log-likelihood ratio tests, with P values corrected for testing on the boundary (Zuur et al. 2009). The

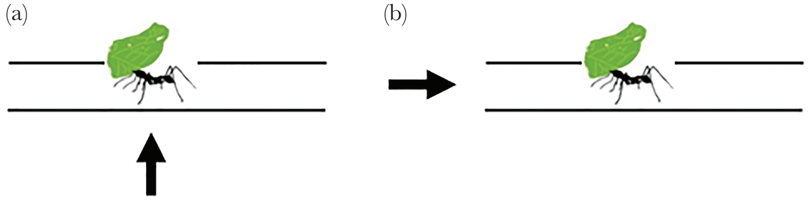

Figure 1

Load position according to trail location in relation to wind direction: (a) perpendicular to wind, where the greatest surface of the load intercepts the wind and (b) parallel to wind, only the thickness of the load intercepts the wind. Arrows indicate wind direction.

proportion of ants that were blown off the trail was analyzed using generalized linear model (GLM) with binomial error distribution of the response variable, with the same fixed factors that for ant speed.

We experimentally assessed the effect of wind by generating wind with computer coolers on 13 trails of 13 nests. The coolers blew wind perpendicular to the ant course. We filmed, for each trail, a 20-cm section with half of it exposed and the other half unexposed to wind until 10 loaded ants were recorded (Supplementary Figure S2). The maximum speed that we could use was 4 km/h because at higher wind speeds ants walked away or passed behind the coolers. In the 2 trail sectors (with and without wind), we measured for each of 126 ants the speed, the number of times that ants were blown off the trail, and the "transition time," that is, the time that each ant spent crossing from a windless sector to a windy sector. The transition time was compared with the time that each individual spent crossing an imaginary line between 2 windless conditions. The transition time depicts the natural situation when ants move along a trail exposed to wind but with sectors protected by vegetation (i.e., windbreaks). We measured ant speed when ants were not blown off the trail. The ant speed and transition time were log-transformed to meet analysis assumptions and analyzed using linear mixed-effect models. Wind condition was considered as fixed factor and nest and ant identity as random factors. We tested whether the random effect was significant using log-likelihood ratio tests, with P values corrected for testing on the boundary (Zuur et al. 2009). The number of times that each ant was blown off the trail was analyzed using generalized linear mixed-effect model with Poisson error distribution of the response variable, wind condition as fixed factor, and nest and ant identity as random factors.

We evaluated correlatively and experimentally whether area, mass, and shape of loads influence wind effect. First, we collected the 10 ants filmed in the experiment with computer coolers and their loads. Because ant size influences its speed (Burd 1983; Hurlbert et al. 2008), in the laboratory, we measured the body length (from the tip of the head to the tip of the gaster) as well as the load mass and took a photo of each load in a stereoscopic microscope. With these photos, we measured the area and perimeter of loads using the software ImageJ®. To control for ant size, we only included ants of 4–5 mm of length in the analyses. We analyzed whether load characteristics influence the effect of wind delaying ants using regression analyses. The response variables were the difference in speed without and with wind, and the presence/absence of ants blown off the trail. As explanatory variable, we used an interception coefficient (IC) of load and calculated as:

$$\mathrm{IC} = \frac{\mathrm{Area} \times \mathrm{mass}}{\mathrm{Shape}}$$

where the load shape was estimated as $\frac{\mathrm{Perimeter}}{\sqrt{\mathrm{Area}}}$, with a value near 4 meaning a square load and higher than 4 indicating an elongated load (Rapoport 1975). The IC increases with a greater potential of loads to intercept more wind, that is, with increments of area and/or mass, and/or squarer shapes. We assumed that 1) wind interception increases with load area; 2) the energy that ants need to maintain the load in equilibrium increases with load mass, so heavier loads should be more unfavorable in windy conditions than lighter loads; and 3) circular or square loads offer more resistance to wind than rectangular loads of similar area because the twisting effect of a force applied to a rotating object, known as torque, is stronger. The effect of IC on the ant's speed was analyzed with a simple linear regression, and on the presence/absence of ants blown off the trail with a logistic regression (0 when ant was not blown off and 1 when was blown off the trail). The data of ant's speed were log-transformed to satisfy the normal and homogeneity assumptions.

To experimentally assess if load selection depended on wind conditions in windy and windless days and moments with and without wind on the same day, we offered paper fragments that differed 2-fold either in area, mass, or shape but not in the other parameters (e.g., same area and mass but different shapes). We used the meteorological data from WindGuru (http://www.windguru.cz/es) and recorded the average wind speed at ground level with a digital anemometer (range of precision: 1.4–108 km/h). Windy and windless days were defined as days characterized by wind and calm separated by 24 h, and moments with and without wind on the same day were defined as windy and windless moments on the same day (wind speed greater than 2 and 0 km/h at the ground level, respectively). The paper fragments were 1) large and small (49 and 25 mm^2; square and 5 mg); 2) light and heavy (5 and 10 mg cut out of paper of 75 and 150 $\mathrm{g/m}^2$, respectively; 60 mm^2 and square); and 3) rectangular and square (20 × 3 and 7.8 × 7.8 mm, respectively; 60 mm^2 and 5 mg). The fragments were soaked with orange juice for at least 1 h and then dried to attract ants (e.g., Röschard and Roces 2002). Paper fragments were placed at the side of trails from different nests and at 1 m from nest entrance. We presented separately the 3 fragment types by couples and replaced them until we achieved 10 repetitions per trail per wind condition, that is, until 10 fragments were picked up by the ants. To evaluate the effect of wind variation among days, we performed this in 14 nests; to evaluate the effect of wind variations on the same day, we repeated this in 12 nests. The removal of each type of paper (response variable) was analyzed using generalized linear mixed-effect models with binomial error distribution. Wind condition and type of paper were considered as fixed factors, and nest identity was a random factor; we run 3 models, one for each type of paper fragment. We expected a statistical significant interaction among the fixed factors if the selection of the type of fragment depends on wind condition. We could not obtain the P value of the random variable because the generalized linear mixed model (GLMM) and GLM are not commensurate; instead of this, we evaluated its standard deviation (Zuur et al. 2009).

To analyze the long-term response to the effect of wind, we assessed cardinal orientations of trails from 43 *A. lobicornis* nests located in El Chocón (windy site) and 38 in La Florida (windless site). We measured the trail direction with respect to the magnetic north and the trail length (meter) in such direction; we also measured the percent of each trail wind-protected by vegetation. With these data, we calculated the grand mean vector for each trail considering all directions and their lengths, or considering only those that had 40% or less of the length protected by vegetation. The grand mean angle is used when data are composed of circular (angle direction of trails) and linear (their associated lengths) measurements. Once we obtained the grand mean angle for each trail with and without vegetation, we analyzed whether trail distribution was uniform (i.e., random) determining the statistical significant of the mean vector r with a Rayleigh's test (Batschelet 1981). A longer mean vector implies greater concentration of the data around the mean and thus less likelihood of the data being uniformly distributed.

Because trail direction may be also influenced by the abundance and quality of resources around the nest (Silva et al. 2013), we estimated the cover of palatable plant species around our sampled nests. We calculated the mean length of trails for each nest and used this mean to place a quadrat in each cardinal point. In El Chocón, we marked a 10 × 10 m quadrat divided into 10 individual units of

1 × 1 m in which the identity and cover (%) of all plant species were recorded. In La Florida, because the plant structure differs from El Chocón (it is a mixture of meadow and Serrano forest), we used a 1 × 1 m quadrat to record the identity and cover (%) of herbaceous species, and a 4 × 4 m quadrat for shrubs and tree species. With these data and the preferred species by *A. lobicornis* in El Chocón and La Florida (Supplementary Tables S1 and S2; Farji-Brener AG and Jofré LE, unpublished data), we obtained the cardinal locations of patches where the cover of preferred plant species was higher than 50%. Then, we counted the number of trails spatially directed or not toward the richest patches, considering an angular variation of ± 30°. For example, if the richest patch was located toward north (0°) and the nest had 3 trails of 25°, 180°, and 300°, we recorded 1 trail as oriented toward the richest patch (i.e., the 25° one) and the other as not oriented toward the richest patch.

RESULTS

Wind effect on foraging: comparative and correlative measurements

Wind decreased the speed of loaded ants traveling along trails perpendicular to the wind direction and without vegetation, but not on perpendicular trails to the wind with vegetation or parallel to the wind without vegetation (GLMM, F = 6.37, P < 0.0001; Figure 2 and Supplementary Table S3). In addition, the wind blew more ants off on trails without vegetation that were perpendicular to the wind or upwind than on trails protected by vegetation or downwind without vegetation (GLM binomial error distribution, X^2 = 485.9, P < 0.0001; Figure 3). The experiment with simulated wind showed similar results; the wind decreased 55% ant speed and increased 28 times the number of times that each ant was blown off the trail (GLMM, transport speed: F = 71.5, P < 0.0001; and number of time that each ant was blown off the trail: X^2 = 79.9, P < 0.0001; Supplementary Figure S3A,B). We also found that ants spent 6.7 s more to cross from a windless to a windy condition than to cross among 2 windless conditions (GLMM: F = 82.5, P < 0.0001; Supplementary Figure S3C).

As expected, the speed of loaded ants depended on load characteristics. Larger, heavier, and more square loads caused higher reduction in speed than smaller, lighter, or more elongated loads (simple linear model [SLM], F = 11.1, P = 0.002, R^2 = 0.21, $y = 0.13x - 0.2$; Figure 4). However, the probability of ants to be blown off the trail did not depend on the area, mass, or shape of loads (GLM binomial distribution, X^2 = 1.3, P = 0.25).

Short-term response: wind effect on load selection

The selection of load according to the area, mass, and shape of fragments varied between windless and windy days, and on the same day between windless and windy moments. In windy days, ants selected against heavy and square fragments, whereas in windless days, they selected heavy over light and square over rectangular fragments (GLMM, heavy vs. light fragments: F = 12.6, P = 0.0004; square vs. rectangular fragments: F = 9.0, P = 0.003; Figure 5 and Supplementary Table S5). Within a day, in windy moments, ants selected against heavy and square fragments, whereas in windless moments, ants selected larger quantity of large, heavy, and square fragments (GLMM, large vs. small fragments: F = 19.1, P < 0.0001; heavy vs. light fragments: F = 3.2, P = 0.001; square vs. rectangular fragments: F = 46.5, P < 0.0001; Figure 5 and Supplementary Table S6).

Long-term response: wind effect on the spatial design of the trail system

Contrary to our expectation, cardinal orientation of trails did not show a clear pattern with respect to wind direction. Considering all trails (with and without surrounding vegetation), we found that in the windless site (mean wind speed ± SE: 6 ± 0.1 km/h) trails were concentrated upwind (mean ± SE: 209 ± 19°, Rayleigh's test, Z = 4.4, P = 0.01, r = 0.2; Figure 6), whereas in the windy site

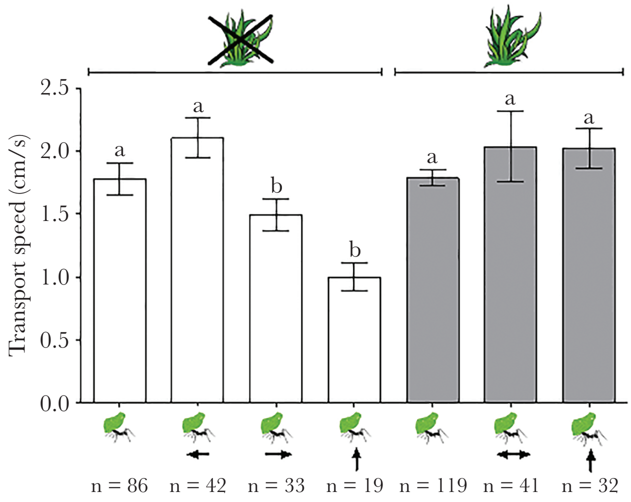

Figure 2
Speed (centimeter per second) of loaded ants (mean ± SE) in windy and windless days, in parallel or perpendicular trails regarding wind direction, and surrounded or not by vegetation. Presence of arrows indicates wind direction with respect to ant walking direction. White bars show trails without vegetation, and gray bars indicate trails surrounded by vegetation. Different letters indicate significant statistical differences (GLMM, F = 6.37, P < 0.0001).

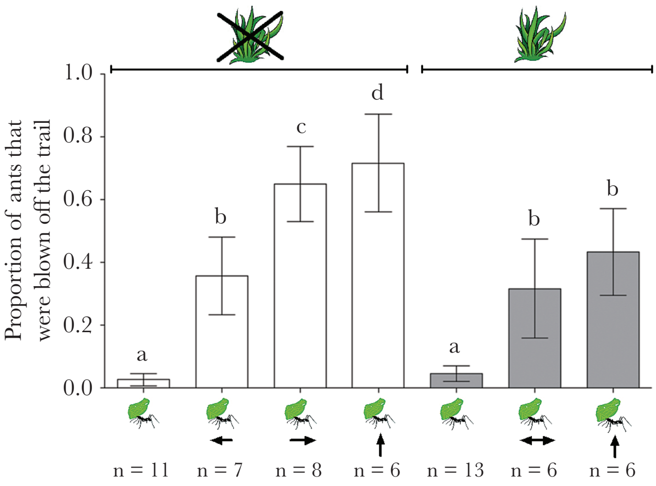

Figure 3
Proportion of ants that were blown off the trail (mean ± SE) in windy and windless days, in parallel or perpendicular trails regarding wind direction, and surrounded or not by vegetation. The presence of arrows indicates the presence of wind and its direction with respect to ant-walking direction. White bars represent trails without vegetation, and gray bars show trails surrounded by vegetation. Different letters indicate significant statistical differences (GLM binomial error distribution, X^2 = 485.9, P < 0.0001).

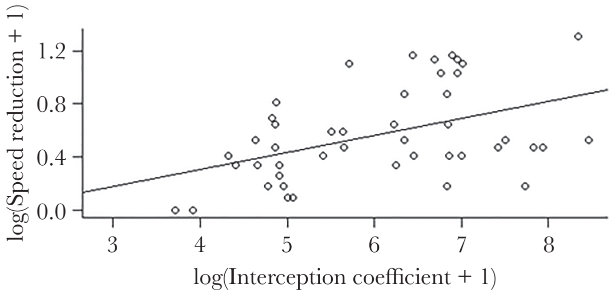

Figure 4
Linear regression for speed reduction of loaded ants with the IC of loads (greater IC implies more wind interception; SLM, $F = 11.1$, $P = 0.002$, $n = 44$; $R^2 = 0.21$, $y = 0.13x - 0.2$).

(mean wind speed ± SE: 20 ± 0.2 km/h) trails were oriented uniformly, but tended to concentrate upwind and downwind (mean ± SE: 55 and $235 \pm 13.9°$; Rayleigh's test, $\mathcal{Z} = 2.1$, $P = 0.1$, $r = 0.2$; Figure 6). On the other hand, considering the orientation of trails with 40% or less of their length protected by vegetation, we found that in the windless site trails were also concentrated upwind (mean ± SE: $217 \pm 14°$, Rayleigh's test, $\mathcal{Z} = 6.8$, $P < 0.001$, $r = 0.5$; Figure 6), and in the windy site, trails were concentrated upwind and downwind (mean ± SE: $59 \pm 7°$ and $240 \pm 7°$, Rayleigh's test, $\mathcal{Z} = 8.3$, $P < 0.001$, $r = 0.4$; Figure 6). In addition, we found that the number of parallel (0–90° and 180–270°) and perpendicular (90–180° and 270–360°) trails with regard to wind direction in the windless and windy sites was similar (all trails: $X^2 = 0.5$, $P = 0.5$; trails without vegetation: $X^2 = 0$, $P = 1$). Finally, trails were not always oriented toward the patches with higher cover of preferred plant species. The percent of trails oriented toward sectors with higher cover of palatable species ranged from 20% to 40% in the windy and windless sites, respectively.

DISCUSSION

Here, we quantified the negative effect of wind on leaf-cutting ants, and analyzed short- and long-term behaviors that could reduce this effect. Wind reduced the speed of loaded ants and thus the rate at which plant material enters the nest. Accordingly, ants selected load characteristics that reduce this effect. However, wind direction does not appear to model the spatial orientation of trails.

In natural wind conditions, loaded ants walked 78% slower and the proportion of ants that were blown off the trails was 93% greater than in windless conditions, whereas in experimental wind conditions, workers reduced their speed by 55% and were blown off the trail 28 times more than in windless conditions. We also found that the spatial variation of wind (as a result of cooler location in a portion of the trail; Supplementary Figure S2) caused an extra delay; ants spent 7 s to cross from a windless to a windy condition. During this time, ants went back and tried to cross the windy zone from a furthest position from coolers. Moreover, in some cases, ants rotated the carried fragment exposing to the wind direction the edge of the load instead its side (see Supplementary MOV. S2). This extra delay occurred naturally when ants travelled along a trail characterized with sectors with and without surrounding vegetation. Altogether, wind increased the time of arrival to the nest and thus strongly decreased the rate of food input. We estimated that the amount of food delivery to the nest was reduced in 50% because of wind. The number of ants per minute in windless conditions was 29 with a mean speed of 1.46 cm/s, whereas in windy conditions, the number of ants was 26 ants/min with a speed of 0.94 cm/s. Considering that the mean length of trails was 13 m and that the mean mass of vegetal fragment was 3.9 mg (data from the experiment with computer coolers and effect of load characteristics on wind effect), the amount of food delivered to nest in windy conditions was 14.5 g/h and in windless condition was 26.8 g/h. Therefore, in this region, wind potentially represents a strong selective pressure for leaf-cutting ants.

Accordingly, ants showed behaviors that reduced this negative effect of wind. Because loads with higher IC (i.e., larger, heavier, and squarer fragments) caused more delay, in windy conditions, ants selected small, light, and rectangular loads; whereas in windless conditions, ants selected large, heavy, and square loads. This suggests that in the absence of the constraints imposed by wind ants can optimize their foraging trips by transporting bigger loads (Rudolph and Loudon 1986) and avoid elongated loads that decrease maneuverability, stability, speed, and transport rate (Röschard and Roces 2002; Moll et al. 2012, 2013). Finally, ants were able to select load characteristics that reduce the negative effect of wind depending on the presence of wind blowing on the same day, suggesting that this behavioral response is flexible and immediate. There are other examples showing how leaf-cutting ants can rapidly adjust their foraging behavior to adverse conditions. For example, when a height constraint is placed 1 cm above part of the trail, ants cut smaller and rounder fragments than in its absence (Dussutour et al. 2009). Also, ants can select fragments by their mass when transporting loads along different trail gradients; for example, on uphill gradients, they transport loads with lower mass, whereas on vertical downhill gradients, they transport heavier loads (Lewis et al. 2008; Norton et al. 2013). Our results offer novel evidence of how leaf-cutter ants adjust their behavior under disadvantageous environmental situations, reinforcing the relevance of behavior plasticity in ants.

Trail characteristics may attenuate the negative effect of wind on ant foraging. We found that wind had no effect on ants that were walking along downwind parallel trails or protected by vegetation. These results are similar to those found in flying organisms; for example, wind only decreases albatrosses' flying speed when they are flying against the wind direction (Weimerskirch et al. 2000) and affects bats' foraging only when wind blows perpendicularly to wind direction in sites that are unprotected by vegetation (Verboom and Spoelstra 1999). Accordingly, we expected that ants inhabiting regions with strong winds avoid building trails perpendicular to the main wind direction. Contrary to our expectation, trails did not show a particular spatial distribution in relation to wind direction, suggesting that trail orientation is modulated by other factors different from wind. An obvious factor that could better explain the spatial design of the trail system is the location of preferred food patches because that is the main goal of the trunk-trail system (Kost et al. 2005; Silva et al. 2013). Surprisingly, most of the trails did not orient toward the patches with higher cover of preferred plant species, possibly because ants did not know location of all resources within their foraging area (Brown and Gordon 2000) and/or because resource quality can vary along time faster than the trail system. On the other hand, the cover of palatable species per se may be a poor estimator of the location of palatable ephemeral resources such as young leaves, flowers, and fruits.

The spatial design of trails (i.e., bifurcation angles) can also respond to a context dependent trade-off between reducing travel time, maintenance cost, and the creation of new trail sections (Farji-Brener et al. 2015). Moreover, cardinal orientation of trails can be affected by trails of neighboring nests or ground

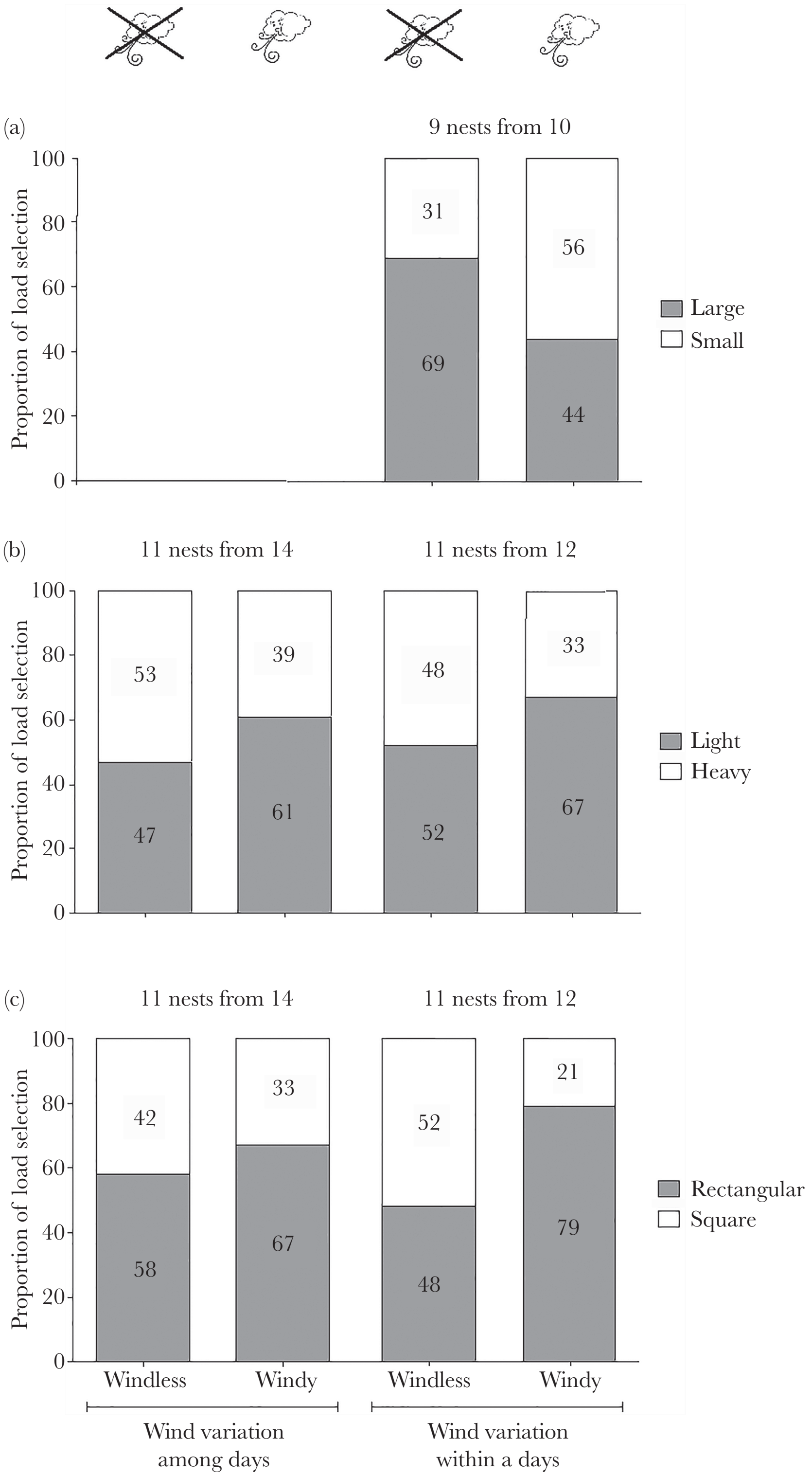

Figure 5
Relative proportion of loads that were (a) large or small; (b) light or heavy; and (c) rectangular or square; in windy and windless days (wind variation among days), and within a day in windy and windless moments (wind variation within a day). Inside the bars are indicated frequencies of selection for every type of paper fragment, and above the bars are indicated the number of nests that responded as the general pattern found, that is showing the same tendency considering all nests together.

characteristics (Brown and Gordon 2000; Farji-Brener et al. 2007). In consequence, the cardinal direction of trails does not respond unequivocally to wind direction and may be modeled by multiple factors. Nevertheless, it is noteworthy that trails mostly unprotected by vegetation were strongly concentrated parallel to the wind direction in both sites (windless site: $r = 0.4$ and windy site: $r = 0.5$). This

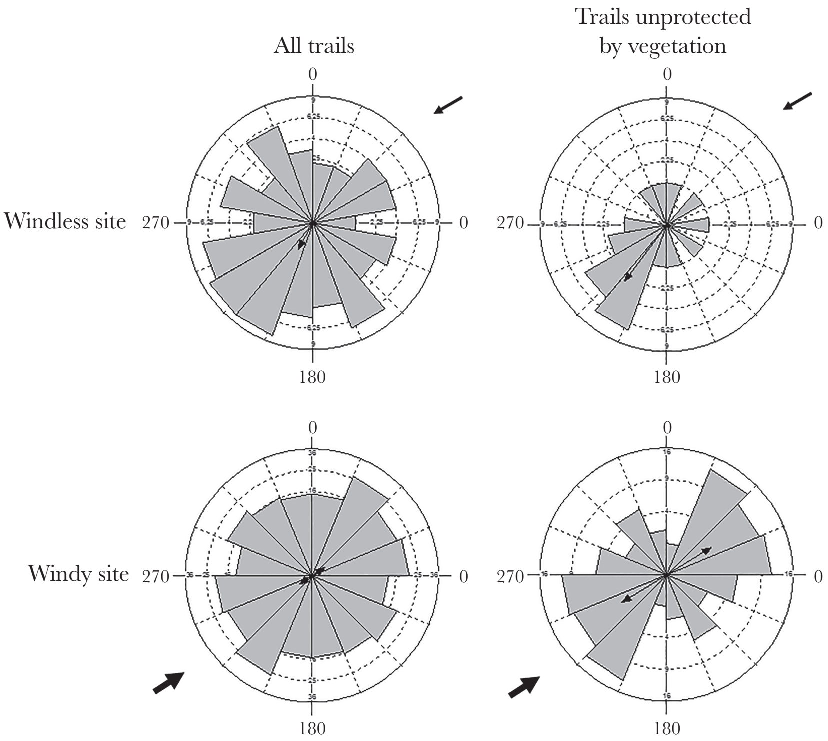

Figure 6

Trail orientation in the windless (upper panels; La Florida, San Luis) and windy sites (lower panels; El Chocón, Neuquén) with regard to magnetic north. Arrows outside circular diagrams represent the prevailing wind direction at El Chocón and La Florida; arrows on the circular diagram indicate the direction and length of the grand means (*r*), considering all trails (left panels; Rayleigh's test, windless site: 209 ± 19°, $Z = 4.4$, $P = 0.01$, $r = 0.2$; windy site: 55 and 235 ± 13.9°, Z = 2.1, $P = 0.1$, $r = 0.2$) or trails with 40% or less of their length protected by vegetation (right panels; Rayleigh's test, windless site: 217 ± 14°, $Z = 6.8$, $P < 0.001$, $r = 0.5$; windy site: 59 and 240 ± 7°, $Z = 8.3$, $P < 0.001$, $r = 0.4$).

result suggests that intensity and prevalence of wind are sufficient to trigger a long-term response both in windy and windless sites. Nevertheless, more studies evaluating persistence of vegetation around trails and ground characteristics are necessary to determine the relative importance of wind on the design of the trunk-trail system.

Our results contribute to a better understanding of the high variation in load characteristics carried by leaf-cutting ants (Fowler and Robinson 1979; Franzel and Farji-Brener 2000), in addition to reaffirming the flexible and short-term response of these ants to adverse climatic conditions (Lewis et al. 2008; Dussutour et al. 2009; Norton et al. 2013). Furthermore, this work may help explaining why leaf-cutting ants show low foraging rate and are uncommon in regions with strong and frequent winds (Cherrett 1972; Hölldobler and Wilson 1990; Farji-Brener and Ruggiero 1994). Some studies have already described how flying and walking organisms change their movement and their extended phenotype (e.g., spider webs) to reduce the negative effects of wind (e.g., Hieber 1984; Wolf and Wehner 2005). However, this is the first study that quantifies the effect of wind in walking insects that move at the ground level and transport loads that magnifies this effect, illustrating how behaviors may mitigate transient environmental conditions that negatively influence foraging.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

This work was supported by Fondo para la Investigación Científica y Tecnológica (FONCYT; PICT-2011-1406). A.M.A. was supported by a fellowship from AGENCIA.

We thank J.F. Minati and L.E. Jofré for help during fieldwork. We thank S. Vargas and 2 anonymous reviewers for helpful comments on an earlier version of this manuscript. We thank Miguel and Martha Luengos for allow us to work in their field.

Handling editor: Glauco Machado

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