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A Breath of Fresh Air in Foraging Theory: The Importance of Wind for Food Size Selection in a Central-Place Forager

Andrea Marina Alma,* Alejandro G. Farji-Brener, and Luciana Elizalde

Laboratorio Ecotono, Instituto de Investigaciones en Biodiversidad–Unidad Ejecutora del Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional del Comahue, Bariloche 8400, Argentina

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abstract: Empirical data about food size carried by central-place foragers do not often fit with the optimum predicted by classical foraging theory. Traditionally, biotic constraints such as predation risk and competition have been proposed to explain this inconsistency, leaving aside the possible role of abiotic factors. Here we documented how wind affects the load size of a central-place forager (leaf-cutting ants) through a mathematical model including the whole foraging process. The model showed that as wind speed at ground level increased from 0 to 2 km/h, load size decreased from 91 to 30 mm^2, a prediction that agreed with empirical data from windy zones, highlighting the relevance of considering abiotic factors to predict foraging behavior. Furthermore, wind reduced the range of load sizes that workers should select to maintain a similar rate of food intake and decreased the foraging rate by ~70% when wind speed increased 1 km/h. These results suggest that wind could reduce the fitness of colonies and limit the geographic distribution of leaf-cutting ants. The developed model offers a complementary explanation for why load size in central-place foragers may not fit theoretical predictions and could serve as a basis to study the effects of other abiotic factors that influence foraging.

Keywords: environmental factors, foraging rate, mathematical model, resource accumulation.

Introduction

Optimal foraging theory establishes how organisms maximize the rate of food delivery or energetic efficiency (i.e., mass or energy per unit of time or energy gained per unit of energy expended, respectively) according to the costs of transport, manipulation, and discovery, among others (MacArthur and Pianka 1966; Pyke et al. 1977). One extension of this theory, the central-place foraging theory (CPFT), considers animals that forage in a patch at some distance and then return resources to a central place (Orians and Pearson 1979). The classical theory predicts the relationship between the size of a food item taken and the travel distance for a variety of taxa, such as ants, passerines, hummingbirds, seabirds, rodents, and humans (Jenkins 1980; Andersson 1981; Bryant and Turner 1982; Tamm 1989; Holway and Case 2000; McAleer and Giraldeau 2006; Houston 2011; Patrick et al. 2014; Wakefield et al. 2014). Although CPFT has been foundational for behavioral ecology, many ecological and environmental factors that affect foraging behaviors, such as predation, social interaction, and temperature, have been overlooked, driving a wedge between empirical data and theoretical predictions (Rozen-Rechels et al. 2015).

Recent studies have tried to resolve some disagreements between empirical data and theoretical predictions about the optimal size of carried food by including biotic constraints on foraging (e.g., Roces 1994; Burd and Howard 2005*b*; Olsson et al. 2008; Bollazzi and Roces 2011; Farji-Brener et al. 2011; Shrader et al. 2012; Rozen-Rechels et al. 2015). For example, Olsson et al. (2008) extended the classical CPFT by considering that predation risk may increase with the distance from the central place. Other works have demonstrated how competition, missed opportunity costs, and social foraging may affect food selection (Shrader et al. 2012; Rozen-Rechels et al. 2015). However, studies about the effects of abiotic factors on loading prey selection are few and limited to evaluations of how these factors affect animal movement not using the CPFT framework (e.g., Bart and Summerlin 2007; Wakefield et al. 2009; Weimerskirch et al. 2012).

Leaf-cutting ants (LCAs) are a good model for studying the effect of environmental factors on resource item selection. They are central-place foragers, conspicuous, and easy to manipulate (Burd and Howard 2005*a*, 2005*b*). LCAs cut vegetal material, carry it back to the nest through a trail system cleared of vegetation, and cultivate a mutualist fungus whose specialized hyphal structures are fed to the colony's larvae (Hölldobler and Wilson 1990). More importantly, these organisms have been found to carry smaller loads than that

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* Corresponding author. Present address: Laboratorio Ecotono, Unidad Ejecutora del Consejo Nacional de Investigaciones Científicas y Técnicas–Universidad Nacional del Comahue, Pasaje Gutiérrez 1125, 8400 S.C. de Bariloche, Río Negro, Argentina; e-mail: almamarina8@gmail.com.

ORCIDs: Farji-Brener, http://orcid.org/0000-0001-7251-3866; Elizalde, http://orcid.org/0000-0002-9929-1957.

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predicted by the CPFT (Kacelnik 1993; Burd 1996, 2000, 2001; Burd and Howard 2005*a*).

Different hypotheses have been proposed to explain why LCAs transport loads below their predicted optimum. First, transporting small leaf fragments increases information transfer and allows workers a higher recruitment rate (Roces 1994; Bollazzi and Roces 2011). Second, workers with larger fragments reduce the walking speed of conspecifics along trails, generating bottlenecks (Farji-Brener et al. 2011). Third, the delivery of small loads reduces the handling time on fungal gardens and facilitates their transfer among fungal chambers (Burd and Howard 2005*b*). Fourth, carrying small loads helps to avoid obstacles through trunk trails (Lewis et al. 2008; Norton et al. 2013). However, abiotic factors may also help to explain this foraging behavior (Rudolph and Loudon 1986; Anderson and Jadin 2001; Alma et al. 2016*a*, 2016*b*).

One abiotic factor that could explain the small size of leaf-cutting ants' loads is wind. Gusts of wind reduce ant speed and can even blow ants off the foraging trail (Rudolph and Loudon 1986; Anderson and Jadin 2001). For example, in windy conditions, the leaf-cutting ant *Acromyrmex lobicornis* decreased its speed by 78%, and the proportion of ants blown off the trail was 93% greater than in windless conditions (Alma et al. 2016*b*). These negative effects of wind on foraging depend on load characteristics: larger, heavier, and more square loads cause a higher reduction in speed than smaller, lighter, or more elongated loads (Alma et al. 2016*b*). Hence, the relation between the load characteristics and the negative effect of wind could explain apparently suboptimal loads.

Although the effect of wind on the foraging activity of leaf-cutting ants has been studied empirically, an analytical framework is still needed to fully understand and quantify the effect of wind on the foraging behavior of LCAs at the colony level. Here we (1) determine whether load size that workers select in nature matches the predictions of optimal foraging theory that incorporates the effects of wind and (2) quantify the wind effect on the foraging rate in an integrated way by taking into account both aboveground foraging behavior and belowground resource processing. We developed a mathematical model based on those proposed by Burd and Howard (2005*a*), because models allow us to evaluate the relative significance of multicausal effects and to make predictions about a system. The model was designed to predict the effect of wind and the load size selected by workers, unifying CPFT, individual ant behavior, the effect of wind, and the underground tasks that determine load size.

Methods

Organisms and Sampling Sites

We worked with the leaf-cutting ant *Acromyrmex lobicornis* because it inhabits regions with strong winds as well as windless regions (Farji-Brener and Ruggiero 1994) and builds its nests in open environments (Gonçalves 1961) where it is easy to follow workers and perform experiments. Sampling was carried out in spring and summer between 2013 and 2015 in El Chocón, Neuquén, in Argentina (39°16′S, 68°47′W). The mean speed of wind is 20 ± 0.2 km/h (±SE), and the maximum is 56 km/h (data source: Autoridad Interjurisdiccional de Cuencas), while at ground level the mean speed of wind is 2.5 ± 1.6 km/h (±SE) and the mean speed of gusts is 4.1 ± 3.8 (±SE) with a maximum of 20 km/h, measured with a digital anemometer (Lutron LM-81AM; range: 0.4–30 m/s; resolution: 0.1 m/s). In addition, some samplings were carried out in Dina Huapi, Río Negro (41°04′S, 71°09′W), where wind regime is similar to El Chocón (annual wind speed mean: 23 km/h; Instituto Nacional de Tecnología Agropecuaria and Sistemas de Producción, Economía y Sociología Rural, Bariloche Airport Meteorological Station).

Model

To determine the load size that maximizes LCA foraging and quantify the global effect of wind on leaf-cutting ants' foraging, we developed a mathematical model based on the work of Burd and Howard (2005*a*). LCAs obtain their food after a fungus processes the vegetal material that workers collect. Hence, their foraging includes the delivery of vegetal material to the nest, distribution of this material to chambers with fungal gardens, and processing to convert it to fungal substrate and implant it among the fungal hyphae. Our model therefore included both the aboveground and belowground tasks (i.e., delivery, distribution, and processing) as well as the effect of wind on these tasks (fig. 1). The studied leaf-cutting ant has a unique fungus chamber of ∼30-cm diameter (Bollazzi et al. 2008). Keeping in mind that *Atta* colonies transfer the vegetal material among chambers and that the unique chamber in *A. lobicornis* is too large to assume that there is no transfer within it, we considered that there are sectors within the chamber where minor workers process vegetal material. We considered that the nest has one entrance and the chamber is divided among two, three, and four sectors connected in linear sequence (fig. 1). We used different numbers of sectors because it is unknown how *A. lobicornis* transfers vegetal material within the nest. Because laboratory colonies of *Atta colombica*, whose chambers have diameters of 12–17 cm, can accumulate a maximum of about 5,000 mm^2 of vegetal material (Burd and Howard 2005*a*, 2005*b*), we considered that each sector has a capacity of 5,000 mm^2 in the case of nests with two or three sectors and 2,500 mm^2 for nests with four sectors. We also assumed that colonies have enough workers to maintain the same maximum processing capacity of leaf material (Burd and Howard 2005*a*).

To explain how we modeled the foraging of leaf-cutting ants, we divided the presentation below into three subsec-

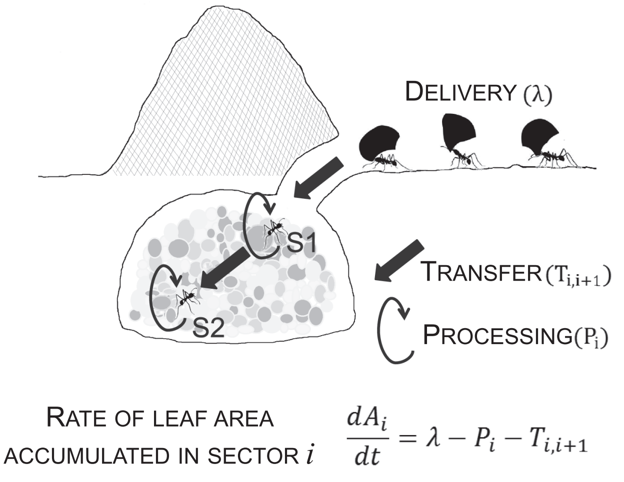

Figure 1: Diagram for the foraging of leaf-cutting ants, including external (delivery) and internal (processing and transfer) processes. Outside, the nest workers transport vegetal fragments that then transfer to other workers inside the nest whose tasks are processing and transferring the vegetal material to another sector of the fungal chamber (in this figure, the chamber has two sectors: S1 and S2). The rate of leaf area accumulated in sector *i* depends on the rate of delivery, processing, and transfer in the way shown in the equation.

tions: (1) complete model, which includes how the foraging tasks were taken into account and units used; (2) delivery rate, which models tasks that happen outside the nest and includes several variables affected by wind; and (3) processing and transfer rates, which model the underground tasks. In each section we explain the biological significance of terms at the beginning and then the mathematical expression that represents each task.

Complete Model. We quantified the foraging rate as the amount of vegetal material (as leaf area) accumulated in each chamber sector per unit of time (rate of leaf area accumulated). This rate depends on the quantity of resources delivered, processed, and transferred into the nest per unit of time (fig. 1). Mathematically, the rate of change of leaf area accumulated in one sector ($\mathrm{d}A_i/\mathrm{d}t$, where A_i is the total leaf area in sector i at any instant of time t) is equal to the leaf area arriving at this sector per unit of time, or delivery rate (λ), minus the leaf area processed into the fungal garden per unit of time, or processing rate (Pr_i), minus the leaf area transferred to the next sector per unit of time, or transfer rate ($T_{i,i+1}$):

$$\frac{\mathrm{d}A_i}{\mathrm{d}t} = \lambda - \mathrm{Pr}_i - T_{i,i+1}. \tag{1}$$

Delivery Rate λ. The delivery rate of resources depends on the load size transported by each worker, the round-trip travel time spent in arriving with a load at the nest, and the number of ants foraging. The time spent by one ant to arrive at the nest depends on their speed and the distance between the nest and the resource. Furthermore, ant speed depends on the load size: ants with larger loads move more slowly than ants with smaller loads (Rudolph and Loudon 1986; Burd 2001). Speed also depends on ant size, but we included only the most common worker size of *A. lobicornis*, 4–5 mm from the tip of the head to the tip of the gaster (Alma et al. 2016*a*). Finally, the delivery rate is regulated by the amount of resources accumulated in the nest (negative feedback control; Burd and Howard 2005*b*).

Mathematically, the delivery rate of resources (λ) is equal to the number of ants foraging (N) multiplied by the load area (a) transported by each worker (i.e., the load size in mm^2) divided by the time spent in going out to the resource and returning to the nest (t_f), all this minus a term representing the negative feedback control, the amount of vegetal material accumulated ($\sum A_i$) multiplied by a constant (k_d) that specifies how accumulated leaf material depresses delivery to the nest:

$$\lambda = \frac{N \times a}{t_f} - k_d \times \sum A_i. \tag{2}$$

We used a k_d value that provided good predictions of load size selection by *A. colombica* (table 1; Burd and Howard 2005*a*).

The time spent by one worker in a foraging round trip is equal to the distance (d) from the nest to the resource divided by the outbound ant's speed (v_0) plus the same distance on the return divided by the ant's laden speed (v_c; $t_f = d/v_0 + d/v_c$). As the laden speed depends on the load size according to $v_c = v_0 - k_v \times a$, where k_v is a constant specifying the effect of load area on ant speed (Rudolph and Loudon 1986; Roces and Núñes 1993; Burd 1996, 2001), the delivery rate is equal to

$$\lambda = \frac{N \times a}{d/v_0 + (d/v_0 - k_v \times a)} - k_d \times \sum A_i. \tag{3}$$

To estimate the distance (d) nest resource, we measured the total length of foraging trails in 39 nests located in El Chocón during the activity period of *A. lobicornis*. We used the median of these lengths as the estimated value of this parameter due to nonnormal distribution (table 1).

Considering that (a) the delivery rate depends on the number of workers foraging and ant speed, (b) both variables are negatively affected by wind (Alma et al. 2016*b*), and (c) our objectives were to quantify the global effect of wind on leaf-cutting ant foraging, we studied the effect of wind empirically. Although it is expected that in regions characterized by strong directional winds trails will not be oriented perpendicular to the prevailing wind direction, cardinal orientation of trails from *A. lobicornis* did not show a pattern

Table 1: Parameter values used in the complete model of foraging (i.e., including external and internal tasks involved) for a nest of the leaf-cutting ant *Acromyrmex lobicornis* with a chamber 30 cm in diameter divided into two sectors connected linearly and sequentially

Symbol	Meaning	Origin	Value and units
d	Distance between the nest and resource	Sampling	10,200 mm
v_o	Outbound unladen ant speed	Sampling	25.4 mm/s
v_i	Inbound ant speed	Sampling	17.2 mm/s
f	Effect of wind on v_o	Sampling	.005
h	Effect of wind on v_i	Sampling	.0007
k_v	Each mm^2 of load reduces ant speed by k_v mm/s	Sampling	.11
g	Increment in the effect of load area per each mm s^1 of wind	Sampling	.0004
k_d	Each mm^2 reduces the delivery of resource by k_d mm^2 s^{-1}	Burd and Howard 2005*b*	.0005
k_t	Constant in equation (7)	Burd and Howard 2005*a*	.2
A_0	Standard value for the difference between A_i and A_{i+1}	Burd and Howard 2005*b*	3,000 mm^2
C	Capacity of a fungal sector	Burd and Howard 2005*a*	5,000 mm^2

with respect to wind direction (Alma et al. 2016*b*). Considering this, we did not vary wind direction in the model. To determine how wind affects the number of workers foraging, we selected 43 nests of similar size (mean ± SE; diameter: 61 ± 19 cm; height: 24 ± 7 cm) and measured the flux of laden and unladen ants during 1 min on all foraging trails of all nests in windy and windless conditions (9.5 and 0 km/h, respectively). We measured the wind speed at ground level with a digital anemometer. To estimate the population of active workers per nest at 1 s, we multiplied the ant flux by trail length and number and divided by trail width, because we measured ant flux as the number of ants crossing an imaginary line of one trail per nest:

$$N = \frac{\text{flux} \times \text{trail length} \times \text{trail number}}{60\ \text{s} \times \text{trail width}}. \tag{4}$$

We used the median of our empirical measurements of trail length, width, and number due to nonnormal distributions of these variables. We analyzed the effect of wind on N using generalized linear mixed models where the response variable was the number of active workers with negative binomial distribution, the fixed factor was the wind speed, and the random factor was the nest (per nest, we had more than one estimation according to trail and wind condition). Since the link function was logarithmic, we retro-transformed the function to an exponential form. The relation between the number of active workers and the wind speed was $N = e^{(5.78-0.0004 \times v_{\text{wind}})}$ (unit of wind speed: v_{wind} mm/s; fixed factor effect: $\chi^2 = 13.92$, $P = .0002$; table A1; tables A1, A2 are available online).

To determine how wind affects unladen ant speed, we filmed one foraging trail from each of 25 nests located in El Chocón in different wind conditions (0–7.5 km/h) for 150 s. In each video, we selected between three and 10 outbound ants of similar size (4–5 mm in length) and estimated their speed by measuring the time that each ant spent crossing 10 cm of the trail. We also measured the wind speed with the digital anemometer during the video. To determine how unladen ant speed decreases with wind, we used generalized linear mixed models where the response variable was the unladen ant speed with normal distribution, the fixed factor was the wind speed, and the random factor was the nest (per nest, we had more than one ant and different wind conditions). The relation between the unladen ant speed and the wind speed was $v_{\text{unladen}} = 25.4 - 0.005 \times v_{\text{wind}}$ (units of speed: mm/s; fixed factor effect: $\chi^2 = 18.8$, $P < .0001$; table A1).

To determine the effect of wind on laden ant speed, we generated artificial wind with computer fans in 13 foraging trails from 13 nests during days without wind (0 km/h). The fans were placed at 5 cm from the trail and oriented so that the artificial wind was blowing perpendicular to the trail. For each trail, we filmed a sector exposed and not exposed to the artificial wind (10 cm in length for each sector). The maximum wind speed at which the ants continued foraging on trails was 4 km/h (wind speed similar to natural wind speed at ground level); at higher wind speeds, ants walked away or passed behind the fans. The anemometer registered 0 km/h at the sector not exposed to the computer fans. From each video, we selected between two and nine ants of similar size (4–5 mm in length) and measured the time that each ant spent crossing 10 cm of trail to estimate their speed. We also removed the 73 selected ants with their loads to weigh the loads in the laboratory. With these data, we estimated the effect of load weight on ant speed in windless and windy conditions. We used generalized linear mixed models where the response variable was the laden ant speed with normal distribution, the fixed factor was the load weight, and the random factor was the nest (per nest, we had more than one ant and different wind conditions; see table A2). Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n0g90 (Alma et al. 2017). With these data, we estimated the effect of load weight on ant speed in windless and windy conditions, and with the results (see the appendix, available online) we could calculate the net rate of resource delivery as

$$\lambda = \frac{\exp(5.78 - 0.0004 \times v_{\text{wind}}) \times a}{\dfrac{d}{25.4 - 0.005 \times v_{\text{wind}}} + \dfrac{d}{(17.2 - 0.0007 \times v_{\text{wind}}) - (0.11 + 0.0004 \times v_{\text{wind}}) \times a}} - k_d \times \sum A_i. \tag{5}$$

Processing and Transfer Rates. Because the underground processes (i.e., the processing and transfer of vegetal material inside the nest) may explain why leaf-cutting ants transport small vegetal fragments (Burd and Howard 2005*a*, 2005*b*) and because we did not know whether the effect of wind would be greater or lower than the effect of these processes, we included these tasks in our model. The process and transfer have already been modeled, and wind does not affect them directly, because these tasks occur inside the nest. Thus, we considered the same parameters and equation used by Burd and Howard (2005*a*, 2005*b*; table 1). They measured the time required for processing fragments of different sizes from the moment they are placed into the nest until the tissue has been implanted among the hyphae. The researchers found that the mean rate of processing a fragment of area a is equal to $p = a^{0.68}/(1{,}088\ \text{mm}^2/\text{s})$. When we consider that the effective number of fragments in the chamber is equal to the amount of accumulated area divided by the area of these fragments (A_i/a) and that every fragment is processed at a rate p, the total rate of processing is $\text{Pr} = p \times A_i/a$. In addition, the colonies have a maximum capacity of vegetal material (C) that can be processed at a given time, so the rate of processing is

$$\text{Pr}_i = p \times \frac{A_i}{a} \text{ if } A_i < C \text{ or } \text{Pr}_i = p \times \frac{C}{a} \text{ if } A_i \geq C. \tag{6}$$

Regarding the rate of transfer among the sectors of the fungal chamber, Burd and Howard (2005*b*) determined by regression analysis that the transference from one sector to the next is described by $T = a \times k_T \times e^{-0.017 \times a}$, where the parameter k_T represents the colony size and their nutritional state, among other conditions (we used the same value as Burd and Howard 2005*a*; table 1). In addition, the researchers assumed that workers are less motivated to transfer between sectors as the difference in vegetal accumulation between one sector and its next decreases, and they scaled the rate of transfer by the difference $A_i - A_{i+1}$ relative to a standard A_0 (the used value was 3,000 mm^2; table 1). Thus, the rate of transfer $T_{i,i+1}$ between one sector and the next (from i to $i + 1$) is equal to

$$T_{i,i+1} = \frac{A_i - A_{i+1}}{A_0} \times a \times k_T \times e^{-0.017 \times a} \text{ if } A_i > A_{i+1} \text{ and}$$

$$T_{i,i+1} = 0 \text{ otherwise.} \tag{7}$$

Model Solution

Once we developed the model including the three foraging tasks (i.e., delivery, processing, and transfer of vegetal material as well as the effect of wind on the delivery of resources), we used the Runge-Kutta method (implementing the deSolve package in R version 3.0.3) to obtain the numerical solutions that simulated 24 h of activity. As modeled by Burd and Howard (2005*a*), harvesting and underground processes take place for 12 h, followed by 12 h of processing and transferring alone. This represents a typical day of activity for *A. lobicornis* (A. M. Alma, personal observation). All values of A_i started in 0 and were updated every 10 s of simulated time. The rate of leaf area accumulated for the system was calculated as the amount of leaf area incorporated into the nest during the 12 h of harvesting.

To determine the load size that maximizes the foraging in windless and windy conditions, we ran the model with wind speeds of 0, 2, and 4 km/h, corresponding to calm, mean speed of wind (2 km/h), and gust speed (4 km/h), for a range of leaf area between 2 and 160 mm^2 until the leaf accumulation in the sectors reached 0. Furthermore, to determine whether the model predicts the real behavior of ants, we analyzed the load area transported by *A. lobicornis* in the field. We selected 10 nests in Dina Huapi and captured 30 laden ants of 4–5 mm in length per nest during a windy day (from 6 to 43 km/h, measured at 1.5 m above ground level). In the laboratory, we photographed the loads in a stereoscopic microscope and estimated the area of every load with the ImageJ software. Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n0g90 (Alma et al. 2017).

To quantify the effect of wind on the foraging rate, we ran the model with different wind speeds (from 0 to 9 km/h) under the assumption that (1) workers transported the same load size in the different wind conditions (i.e., they did not adjust their load size) or (2) workers adjusted their load size to maximize the foraging rate, thus minimizing the negative effect of wind if this was present (Alma et al. 2016*a*). For the first scenario, we used the median of load area that workers transported naturally and the load size predicted by the model in windless conditions, while for the second scenario, we used the load area that maximized the foraging rate according to the model for wind speeds of 0, 1, 2, 3, and 4 km/h (for the model script, see the supplemental material, available online[1]).

Results

Optimal Load Size

In natural windy conditions (~2–4 km/h), workers of 4–5 mm in length transported loads of 40 ± 1.54 mm^2 in area

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[1] Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

(mean ± SE) with a median of 34 mm^2 (fig. 2). According to the model, the load size that maximized the relative rate of leaf area accumulation was 91, 30, and 17.5 mm^2 for wind speeds of 0, 2, and 4 km/h, respectively (fig. 3). This result indicates a match between the empirical median (34 mm^2 for winds of 2–4 km/h) and the model prediction (30–17.5 mm^2 for winds of 2–4 km/h).

In addition, we found that wind reduced the range of load sizes that workers could select and still maintain a similar rate of resource accumulation (fig. 3). For example, in windless conditions, workers could transport loads between 60 and 120 mm^2 and maintain a relative foraging rate of at least 0.8, while in winds of 2 km/h, they could maintain at least that same relative rate only by transporting loads between 20 and 40 mm^2.

Effect of Wind on Foraging Rate

Wind negatively affected the amount of leaf area accumulated in nests with gardens of two, three, and four sectors whether workers did or did not adjust their load size (fig. 4). The amount of resources accumulated in the nest decreased exponentially as wind speed increased. For example, nests with two sectors whose workers adjusted their load size to wind of 1 or 2 km/h accumulated ~68% and ~82% less, respectively, than in windless conditions. Furthermore, the negative effect of wind was larger for nests with the chamber divided into a larger number of sectors. For example, comparing nests with two sectors with nests with four, we found that the first accumulated ~68% less when wind increased from 0 to 1 km/h, while the second accumulated ~74% less.

We found that when workers were allowed to adjust their loads, colonies accumulated more resources compared to a scenario where workers were not (fig. 4). In windless conditions, the adjustment increased the accumulated area by 115% compared to a scenario where workers transported loads of 34 mm^2 (empirical data; see fig. 2), while in windy conditions the increment was ~10%, 3%, and 121% for winds of 1, 2, and 3 km/h, respectively. Even when wind was 4 km/h, transporting loads of 34 mm^2 did not allow the colonies to accumulate resources because of restrictions imposed by wind on laden ant movement (fig. 4). In the scenario where workers transported loads of 90 mm^2 (model result without wind; see fig. 3), foraging rate decreased to 0 when wind reached 1 km/h.

Discussion

In this work, we developed a mathematical model that allowed us to widen the classical central-place foraging theory by including the effect of one environmental factor: wind. In particular, we evaluated the load size that maximizes the foraging rate in windless and windy conditions considering the three tasks involved in LCA foraging, the delivery of resources and their processing and transfer inside the nest, as well as the effect of wind. We found that with winds of 2 and 4 km/h at ground level, the optimal load size is reduced by 67% and 81%, respectively. We also found that the model's predictions about the optimal load size are consistent with

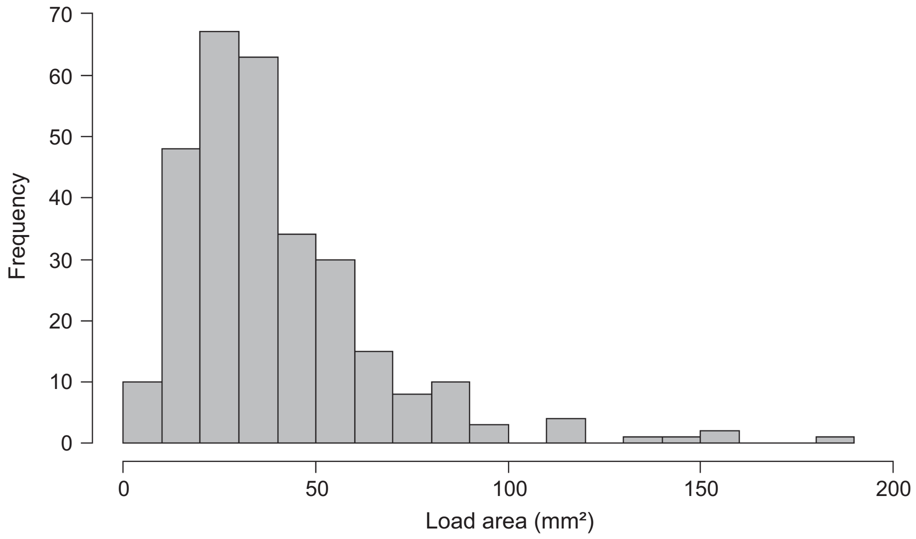

Figure 2: Histogram of the load size transported by workers of 4–5-mm length in the field under winds of ~2–4 km/h (mean ± SE: 40 ± 1.54 mm^2; median: 34 mm^2). Data underlying figure 2 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n0g90 (Alma et al. 2017).

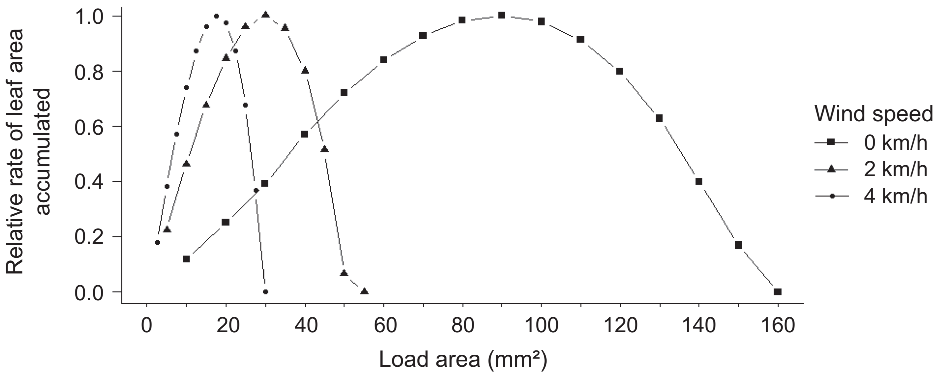

Figure 3: Relationship between load area and relative rate of leaf area accumulated (the rate of leaf area accumulated divided by the maximum for every condition) for a nest with one chamber of 30-cm diameter divided into two sectors connected linearly and sequentially during 12 h of foraging. Symbols represent different wind speeds (0, 2, and 4 km/h). Parameter values are detailed in table 1. We found the same behavior for nests with achamber divided into three and four sectors.

those observed in the field. In addition, the model allowed us to measure the effect of wind in a comprehensive way, considering all the foraging tasks, and to quantify the advantages of an individual strategy used by leaf-cutting ants to mitigate the negative effect of wind (i.e., selections of particular load sizes; Alma et al. 2016*a*).

The load size predicted by the model and the size found in the field study were similar (30 and 34 ± 1.54 mm^2, respectively; median ± SE). This suggests that the model itself and the values of the parameters used are a good approximation of leaf-cutting ant foraging in nature. In addition, it suggests that the processing and transfer tasks in *Acromyrmex* are similar to those described in *Atta*, since we used some parameters derived directly from *Atta* foraging (Burd and Howard 2005*a*, 2005*b*). Furthermore, when workers transported loads of 34 mm^2, wind speeds higher than 4 km/h reduced the rate of resources accumulated completely. This also compares well with previous studies (Alma et al. 2016*a*, 2016*b*), where we observed that winds stronger than 4 km/h caused ants to either walk away from the trail or go behind the fans used to generate artificial wind. However, the model may show some limitations.

One of the limitations is that the model considers only the most abundant medium worker size class (4–5 mm in length), although leaf-cutting ants are polymorphic (Hölldobler and Wilson 1990). As a consequence, the effect of wind may be overestimated. Colonies can reduce the negative effect of wind by 32% by assigning larger foragers that are less affected by wind and can deliver larger loads to the nest (Wetterer 1994; Alma et al. 2016*a*). On the other hand, the model considers nests with only one entrance connecting with its interior, while *Acromyrmex lobicornis* colonies can have up to seven foraging nest entrances (A. M. Alma, personal observation). Finally, our model assumes that ants have a resource supply broad enough to allow them to select load sizes from 17.5 to 90 mm^2. The sampling site (Patagonia) is characterized by an abundance of plants with small leaf sizes, so it is possible that the available resources restrict the load size selection. Despite these limitations, the results show that the model is a good approximation of what happens in nature, offering an alternative or complementary explanation about why leaf-cutting ants transport loads smaller than expected by the optimal foraging theory.

The consistency between the load size predicted by the model and the load size that workers selected naturally suggests that leaf-cutting ants optimize their foraging according to the most frequent wind speed and that the frequency of the gusts is insufficient for affecting worker behavior. We found that the best model to predict the load area of *A. lobicornis* is the one with winds of 2 km/h, values that compare well with the mean speed of wind at ground level in the study site (2.5 ± 1.6 km/h; mean ± SE). This is expected because gusts of wind affect the worker movement for only a few seconds and are less predictable than the mean speed of wind. In consequence, *A. lobicornis* in Patagonia would be able to reduce the negative effect of wind and optimize resource gain by adjusting their load size at the most frequent (i.e., predictable) wind condition.

It has previously been discovered that leaf-cutting ants selected smaller, lighter, and more square fragments (that offer less resistance to wind) in windy than in windless conditions (Alma et al. 2016*b*). Our results show that this individual strategy allows colonies to accumulate more resources that could increase their fitness. Therefore, it is expected that leaf-cutting ants have the ability to detect wind to accurately adjust their load size. Other insects, such as crickets and cockroaches, detect wind with appendixes called cerci (Palka et al. 1977; Dagan and Volman 1982; Jacobs et al. 2008; Miller et al. 2011; Ogawa and Oka 2015). Although it is unknown how leaf-cutting ants detect the intensity and direction of

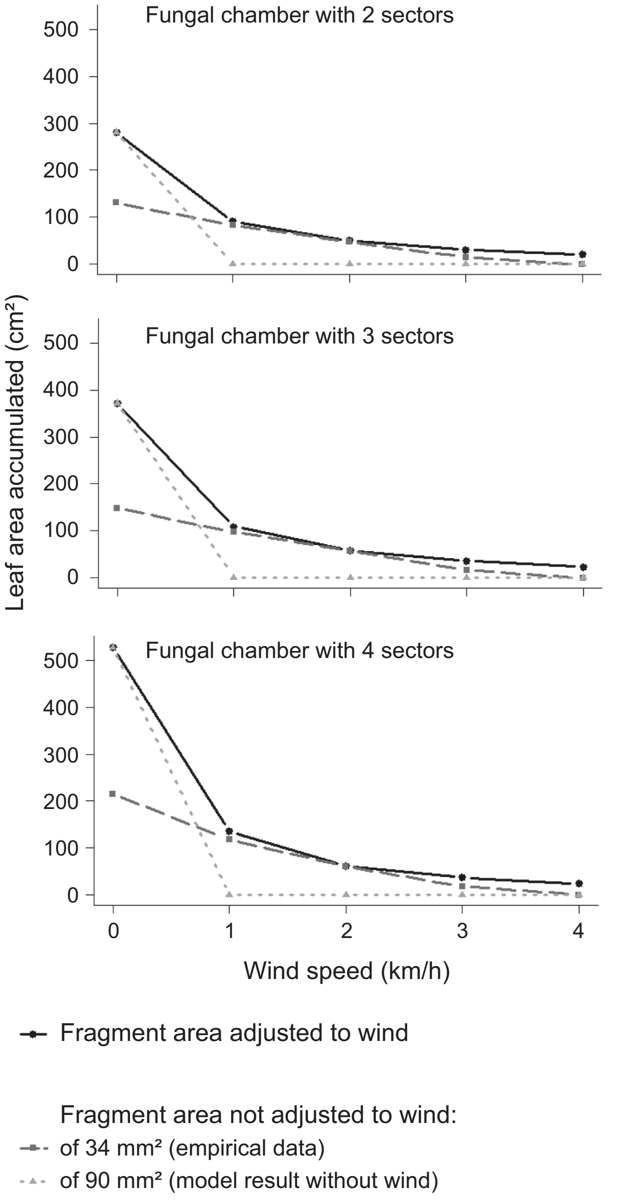

Figure 4: Relationship between wind speed (km/h) and amount of leaf area accumulated (cm^2) for a nest with one chamber divided into two, three, and four sectors connected linearly and sequentially during 12 h of foraging. The solid black line represents the scenario where workers adjusted their load size to wind conditions (model run with load area of 90, 45, 30, 22.5, and 17.5 mm^2 for wind speeds of 0, 1, 2, 3, and 4 km/h, respectively), while the dashed and dotted lines represent the scenario where workers transported the same load area for different wind conditions (34 and 90 mm^2). Parameter values are detailed in table 1.

wind, they orient upwind to odor stimuli by a system located in their antennal lobules (Littledyke and Cherrett 1978; Kleineidam et al. 2005; Kelber et al. 2010; Kuebler et al. 2010). To understand how these ants respond to wind, it is necessary to determine how they detect it, which organs are responsible, and how fast they can adjust their load size while cutting a vegetation fragment according to this environmental factor.

Wind negatively affected the amount of resources that model colonies can accumulate and, more surprisingly, reduced the range of load sizes that workers could select to maintain the foraging rate between 80% and 100% of its maximum. Thus, in windy conditions, workers would have less flexibility to cut or select their loads. This leaf-cutting ant species builds a nest mound composed of primarily vegetal material more than other resources (A. M. Alma, personal observation). These materials are of key importance in regulating the climatic conditions within the nest (Farji-Brener 2000; Bollazzi et al. 2008), but wind limits the transport of bigger loads. Thus, it is possible that beside its negative effect on foraging, wind could also negatively affect nest mound construction and repair. In favor of this hypothesis, in summer (when wind is stronger and more constant), ants use small pieces of debris from their refuse to repair mounds, while in spring, autumn, and winter, ants repaired their nest with larger vegetal material (Farji-Brener and Tadey 2012). Therefore, wind could affect colony fitness because of its negative effects on the ability of workers to accumulate resources and maintain a suitable temperature and humidity for their fungus culture.

Considering that winds of 2 km/h decreased the amount of resources accumulated in the model by more than half and that wind speed increases toward the south in Argentina (Spinadel 2009), wind could limit the austral distribution of this species in particular (which is the leaf-cutting ant species with the southernmost distribution; Farji-Brener and Ruggiero 1994) and the geographic distribution of the leaf-cutting ants in general. Some preliminary evidence supports this hypothesis. First, *A. lobicornis* nests built above the base of plants grow faster than nests built over neck soil (Farji-Brener 2000; Farji-Brener et al. 2003), and nest density increases in zones with dense vegetation that baffles wind (Farji-Brener 1996). Independent of other alternatives (structural support and higher palatable plant species; see Farji-Brener 1996, 2000; Farji-Brener et al. 2003), in windy conditions, vegetation around foraging trails allows workers to walk as fast as in windless conditions (Alma et al. 2016*b*). In this way, nests can grow faster under plants and attain higher density in areas with many plants, because vegetation protects them against wind and reduces the negative effect of wind. Second, wind affects the dispersion capacity of ant queens (Vogt et al. 2000), which could have negative consequences for colonization of new sites. Third, less windy zones present greater richness of leaf-cutting ant species (fig. A1, available online). Although the role of temperature constraining the distribution of leaf-cutting ants has been studied (Farji-Brener and Ruggiero 1994), here we offer a basis to consider that wind could also limit the advance of leaf-cutting ants in more austral regions or windy zones.

Movement and foraging of many central-place forager species are negatively affected by wind. Most previous studies have focused on how the flight speed and costs of seabirds are negatively influenced by wind. For example, energy and time costs of gliding for albatrosses depend on wind direction, and their flight speed decreases as the wind speed increases (Weimerskirch et al. 2000; Wakefield et al. 2009). In addition, wind decreases the capture rate, influences the capture method and foraging habitat, and increases the metabolic rate of terns, gulls, and fulmars (Taylor 1983; Furness and Bryant 1996; Gilchrist et al. 1998). Nevertheless, many nonflying organisms can also be affected by wind, especially in a region such as Patagonia, where gusts of wind can reach up to 100 km/h. Although our model has some particularities of leaf-cutting ant biology (e.g., processing and transfer of vegetal material inside the nest), we think that it could be used as a basis for model foraging of other central-place foragers beside ants.

The effect of wind on the foraging activity of leaf-cutting ants had already been studied empirically (Alma et al. 2016*a*, 2016*b*); however, this mathematical model allowed us to quantify the effect of wind in a global way, considering its effects on the delivery rate, including the underground tasks that determine the load size and hence the rate of resource accumulated (Burd and Howard 2005*a*, 2005*b*). Although it is necessary to adjust some parameter values, our model could serve as a basis to study the effects of other environmental (e.g., temperature, rain, light), biotic (e.g., parasitoid attack, competitors), or anthropic (e.g., pesticides) factors that influence the leaf-cutting ants' foraging or other central-place foragers beside ants. These potential uses will allow predictions of the foraging behavior of central-place foragers with ecological and economic importance in a wide range of scenarios, illustrating how environmental factors can affect the predictions of the optimal foraging theory.

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