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Coexisting in harsh environments: temperature-based foraging patterns of two desert leafcutter ants (Hymenoptera: Formicidae: Attini)

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Abstract

Dominant herbivores, like leafcutter ants, have a strong impact on the ecosystems they inhabit. Understanding which factors regulate their foraging rates is crucial for understanding ecosystem dynamics. In desert habitats, environmental factors, such as temperature, play a major role in regulating ants' behavior. We studied the role of ground temperature in regulating daily and seasonal activity patterns of two coexisting leafcutters ant species, *Acromyrmex lobicornis* (EMERY, 1888) and *A. striatus* (ROGER, 1863), in the Monte desert of Argentina. We measured the variations in activity levels and soil temperature every two hours throughout the day in colonies of both species every season for two consecutive years. Temperature was a good predictor of both the timing of colony activation (the onset and end of their daily foraging activities) and foraging intensity (the number of workers devoted to foraging tasks). However, temperature affected each species differently: *Acromyrmex lobicornis* foraged at lower temperatures (10 - 35 °C) than *A. striatus* (27 - 45 °C). Our results suggest that these two species have different thermal tolerance ranges that result in temporally separated foraging activities. We suggest that interference competition may have driven this temperature and temporal specialization in these two sympatric species, given their similar sizes and diets. Field observations of activity vs. temperature in allopatry, and behavioral tests in controlled conditions should provide further evidence to test this hypothesis.

Key words: Leafcutter ants, *Acromyrmex*, foraging, herbivory, temperature.

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Introduction

Herbivores are a fundamental part of almost every ecosystem (HUNTLY 1991). They can directly affect the abundance and dynamics of plant species (e.g., OLFFA & RITCHIEB 1998, WIRTH & al. 2008, SUZUKI & al. 2013, LEZAMA & al. 2014, MUTHONI & al. 2014), and even impact whole ecosystems via other trophic and non-trophic indirect effects (MOTHERSHEAD & MARQUIS 2000, PRINGLE & al. 2007). Knowing which factors regulate herbivory is crucial for understanding ecosystem dynamics and the characteristics that promote ecosystem resilience.

Leafcutter ants are the dominant native herbivore in the Neotropics both in terms of their abundance and the amount of plant biomass they harvest (HÖLLDOBLER & WILSON 1990, WIRTH & al. 2003). For example, some species of leafcutter ants, like *Atta laevigata* (SMITH, 1858) and *Atta sexdens* (LINNAEUS, 1758), can consume up to 17% of the foliar biomass produced annually in the temperate savannas of South America (COSTA & al. 2008). Such intense herbivory pressure by leafcutter ants can lead to changes

in the structure, composition and dynamics of plant communities (WIRTH & al. 2003, HÖLLDOBLER & WILSON 2011). For example, foraging by leafcutter ants affects sapling density of several tree species in tropical forests (VASCONCELOS & CHERRET 1997, RAO & al. 2001), and can even lead to the occasional death of adult trees (ROCKWOOD 1975).

Most studies on the factors affecting herbivory rates by leafcutter ants focus on species that live in tropical ecosystems. Activity patterns of tropical species (such as *Atta cephalotes* (LINNAEUS, 1758), *Atta sexdens*, *Atta laevigata*, and *Atta colombica* GUÉRIN-MÉNEVILLE, 1844) are mostly regulated by precipitation regimes and resource availability (e.g., LEWIS & al. 1974, ROCKWOOD 1975, VASCONCELOS 1990, FARJI-BRENER 2001). Yet leafcutter ants also play an important role as herbivores throughout the arid and semi-arid regions of South America (FOWLER & al. 1986, BERTILLER & al. 2009). In contrast to tropical regions, these temperate deserts are characterized by pro-
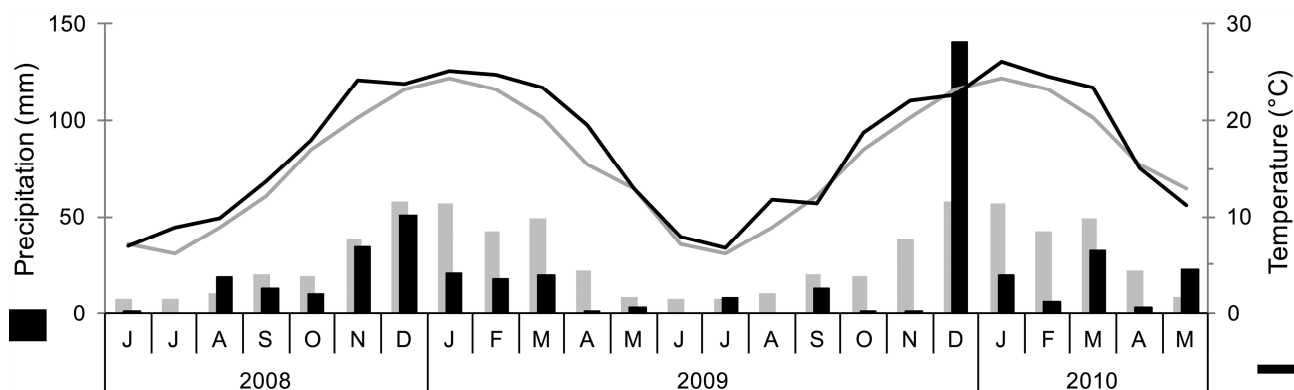
Fig. 1: Monthly precipitation (black bars) and average monthly temperature (black line) at the Biosphere Reserve of Ñacuñán, Argentina, during the two years of sampling from June 2008 to May 2010. Historical averages of monthly precipitation (grey bars) and monthly temperature (grey line) from 1972 to 2012 are also shown for reference. Data retrieved from the records of the reserve's weather station.

nounced seasonality and wide daily variations in temperature, which may regulate ant foraging activity. Two studies on leafcutter ant species from the Sonoran Desert (the northern boundary of their worldwide distribution) showed that *Atta mexicana* (SMITH, 1858) and *Acromyrmex versicolor* (PERGANDE, 1893) have clear foraging preferences related to soil temperature (GAMBOA 1976, MINTZER 1979). Despite their ecological relevance, still little is known about what regulates the herbivory rates of those species of leafcutter ants that live in the temperate deserts of South America.

Two species of leafcutter ants coexist in the Monte desert of Argentina: *Acromyrmex lobicornis* (EMERY, 1888) and *A. striatus* (ROGER, 1863). Both species use the same habitat, are similar in size, and share very similar dietary requirements (NOBUA-BEHRMANN 2014). As with most ectotherms inhabiting desert environments, abiotic conditions (such as temperature) are likely to play a predominant role in regulating the activity of these desert ants (WHITFORD & ETTERSHANK 1975). Alternatively, the avoidance of competitive interactions could also exert a strong influence on the foraging schedule of ants, resulting in complementary daily activity patterns (CERDÁ & al. 1998). When such temporal niche partitioning happens, dominant ants typically forage when temperatures are moderate, forcing subordinate species to forage at more extreme temperatures (e.g., CERDÁ & al. 1997, 1998, BESTELMEYER 2000, RETANA & CERDÁ 2000, ALBRECHT & GOTELLI 2001, CERDÁ 2001, THOMAS & HOLWAY 2005).

Our study focuses on the relationship between soil temperature and the foraging rates of two dominant sympatric herbivores of the arid central Monte desert: the leafcutter ants *Acromyrmex lobicornis* and *A. striatus*. Specifically, we asked: (1) Do the patterns of foraging activity of these herbivores relate to the daily fluctuations in soil temperature? (2) How does each of the two species respond to the restrictions imposed by daily and seasonal changes in temperature? And (3) given that these ants share both diet and habitat, is there evidence that competitive interactions might also be influencing their foraging patterns? Understanding the factors that affect these herbivore's foraging patterns is an important step into comprehending the factors influencing trophic dynamics in South American desert ecosystems.

Methods

This study was carried out at the Biosphere Reserve of Ñacuñán (34° 03' S, 67° 54' W, Mendoza Province, Argentina), in the central portion of the Monte desert. The main habitat in the reserve is an open woodland of *Prosopis flexuosa*, where trees are scattered within a matrix of perennial tall shrubs (mostly *Larrea divaricata*, but also *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa*, and *Larrea cuneifolia*), low shrubs (*Lycium* spp., *Mulguraea aspera*, and *Acantholippia seriphioides*), and perennial grasses (e.g., *Jarava ichu*, *Trichloris crinita*, *Pappophorum* spp., *Sporobolus cryptandrus*, *Aristida* spp., *Digitaria californica*, *Setaria leucopila*). Tree, shrub and grass cover is relatively constant throughout the year. On the other hand, forb cover (e.g., *Chenopodium papulosum*, *Phacelia artemisioides*, *Parthenium hysterophorus*) is higher during spring and summer, and highly variable from year to year. Ñacuñán's climate is dry and highly seasonal. Mean annual temperature is 15.9 °C (1972 - 2004) and mean annual rainfall is 342 mm with high inter annual variation (range: 91 - 585 mm; 1972 - 2004). Seventy-five per cent of the rainfall occurs in spring and summer (October - March; Fig. 1).

Acromyrmex lobicornis and *A. striatus* have a relatively ample distribution in South America, from the southern regions of Brazil and Bolivia to the center-south of Argentina (FARJI-BRENER & RUGGIERO 1994). We used the keys developed by KUSNEZOV (1956) to identify these two species in our study site, where both are relatively abundant (CLAVER & FOWLER 1993). *Acromyrmex lobicornis* colonies are comparatively large (~ 10,000 workers: JOFRÉ & MEDINA 2012) and forage in columns, with well-defined foraging trails. In contrast, *A. striatus* colonies are relatively smaller and have more relaxed foraging trails (NOBUA-BEHRMANN 2014). Both species show a generalist and opportunist diet, and harvest a high percentage of the available plants in the region (NOBUA-BEHRMANN 2014).

During two years (from August 2008 to May 2010), we estimated activity levels in 9 - 11 *Acromyrmex lobicornis* and *A. striatus* colonies located inside the reserve. We revisited study colonies four times each year, during February (summer), May (autumn), August (winter), and November (spring) for a total of eight sampling bouts (one

for each season-year combination). When one or two colonies ceased their activity between visits (presumably due to colony death or change of nest location), we replaced them with new colonies in order to maintain a similar number (~ 10) of colonies sampled across seasons. There was a total of three such replacements in *A. lobicornis* colonies and eight in *A. striatus* colonies over the course of this study.

We measured the foraging activity of each colony every two hours for a whole day in each season. We counted the total number of foragers (ants carrying a food item) returning to the nest during a five-minute period and noted the presence or absence of workers performing nest maintenance tasks (i.e., transporting soil or litter out of the nest). We also measured soil surface temperature near the nest entrance with a digital thermometer (range: -50 - 150 °C, precision: 1 °C) buried a few millimeters under the soil surface to avoid direct sunlight on the sensor.

We estimated the ranges of temperatures at which *Acromyrmex lobicornis* and *A. striatus* colonies were active in each sampling bout by averaging the range limits at which each colony was found foraging. For each colony, we also determined the temperature at which it showed its maximum activity (number of returning ants / 5 minutes). We compared colonies' temperature of maximum activity among species and seasons with a two-way ANOVA. We used a Fisher's Least Significant Difference (LSD) test to compare all species by season combinations. Additionally, we used t-tests to compare the maximum activity levels between colonies from the same species sampled in the same season but in different years.

We evaluated two aspects of soil temperature effects on ant foraging activity at a colony level: a threshold response (foraging / not foraging) and a graduated response (number of foragers per five minutes). For the first evaluation, we considered two possible states of a colony: active (with foragers returning to the nest) or inactive (without foragers returning to the nest for at least 5 minutes). We modeled colony activation as a function of temperature using a logistic regression model that included soil temperature (as both linear and quadratic terms) and season (categorical factor with three levels: summer, spring and autumn) as fixed effects, and colony identity and sampling bout as random effects.

For the second analysis, we considered the number of foragers entering the nest during a five-minute period as the response variable. Colonies differed in their size (and therefore in the total number of foragers they have). To be able to compare colonies of different sizes, we created a standardized activity index that ranged from 0 to 1 by dividing each observed activity value by the colony's maximum activity value. We excluded colonies that showed maximum activity < 10 ants / 5 min and had less than three positive records of external activity in a season. For modeling purposes, we also excluded soil temperatures for which we found no activity for each species (activity ranges were 9 - 42 °C for *Acromyrmex lobicornis*, 14 - 52 °C for *A. striatus*). We modeled relative activity levels as a function of soil temperature (as both linear and quadratic terms) and season as fixed effects, and colony identity as a random effect. For this model, we used the identity link function, which assumes normally distributed errors. In both analyses we estimated model parameters using

maximum likelihood to minimize the loss function and the number of explanatory variables included. To simplify our models, we tested the significance of each candidate model and its fixed effects with sequential χ^2 tests that compared the difference in the loss function between the focal model and the previous (more complex) model. We sequentially eliminated variables until no further variables could be deleted without a statistically significant ($p < 0.05$) loss of fit. We used the same procedure (comparison of loss function value with a reduced model without the focal term) to estimate the relevance of explanatory variables in the final models. We used the functions *glmer* and *lme* (included in *lme4* package) of the statistical software R (R DEVELOPMENT CORE TEAM 2012, BATES & al. 2013). We estimated the goodness of fit of the most parsimonious model with a pseudo-R^2 value that compares the likelihood of the model with the likelihood of a null model that does not include any of the fixed nor random effects (KRAMER 2005).

Results

During each sampling bout, all colonies of the same species showed similar daily and seasonal foraging patterns: similar timing of foraging onset, peak and end. We observed variation in foraging intensity (i.e., the number of workers foraging) among colonies, most likely related to differences in colony size. Besides the fact that some colonies were replaced during the length of this study, average maximum activity did not show significant differences among comparable sampling bouts for each species (comparing *Acromyrmex lobicornis* nests in spring: $T_{18} = 0.82$, $p = 0.424$; summer: $T_{17} = 0.01$, $p = 0.993$; and autumn: $T_{18} = -1.04$, $p = 0.314$; and comparing *A. striatus* nests in spring: $T_{17} = 1.90$, $p = 0.074$; summer: $T_{18} = 1.00$, $p = 0.323$; and autumn: $T_{13} = 0.80$, $p = 0.436$).

Seasonal activity patterns were consistent among years. *Acromyrmex lobicornis* colonies actively foraged from spring to autumn, with occasional external activity during winter (Fig. 2). *Acromyrmex striatus* colonies were active mainly during spring and summer, with no signs of foraging activity during winter (Fig. 2). Foraging intensity was highest during spring and summer for both species (up to 150 ants / 5 minutes in *A. lobicornis* colonies, and 90 ants / 5 minutes in *A. striatus* colonies). During autumn, *A. lobicornis* colonies still showed considerably high foraging activity (up to 80 ants / 5 minutes), while *A. striatus* colonies showed very scarce activity (< 15 ants / 5 minutes in any single colony; Fig. 2). Daily and seasonal variations in nest maintenance activity were broadly similar to each species' foraging activity patterns, though spanning larger time ranges than their foraging activity (starting earlier and finishing later; Fig. 2).

During spring and summer, *Acromyrmex lobicornis* colonies foraged mostly during the night, starting at dusk and continuing for up to 16 hours until next morning (Fig. 2). On the other hand, foraging activity in *A. striatus* colonies was exclusively diurnal with 4 - 6 hours of foraging during the morning and 4 hours in the afternoon, avoiding the hotter midday. During the hottest months, the overall daily foraging patterns for these two species appear complementary: *A. striatus* daily foraging activity begins in the mornings when *A. lobicornis* colonies are ceasing their foraging activity cycle. Furthermore, the end-
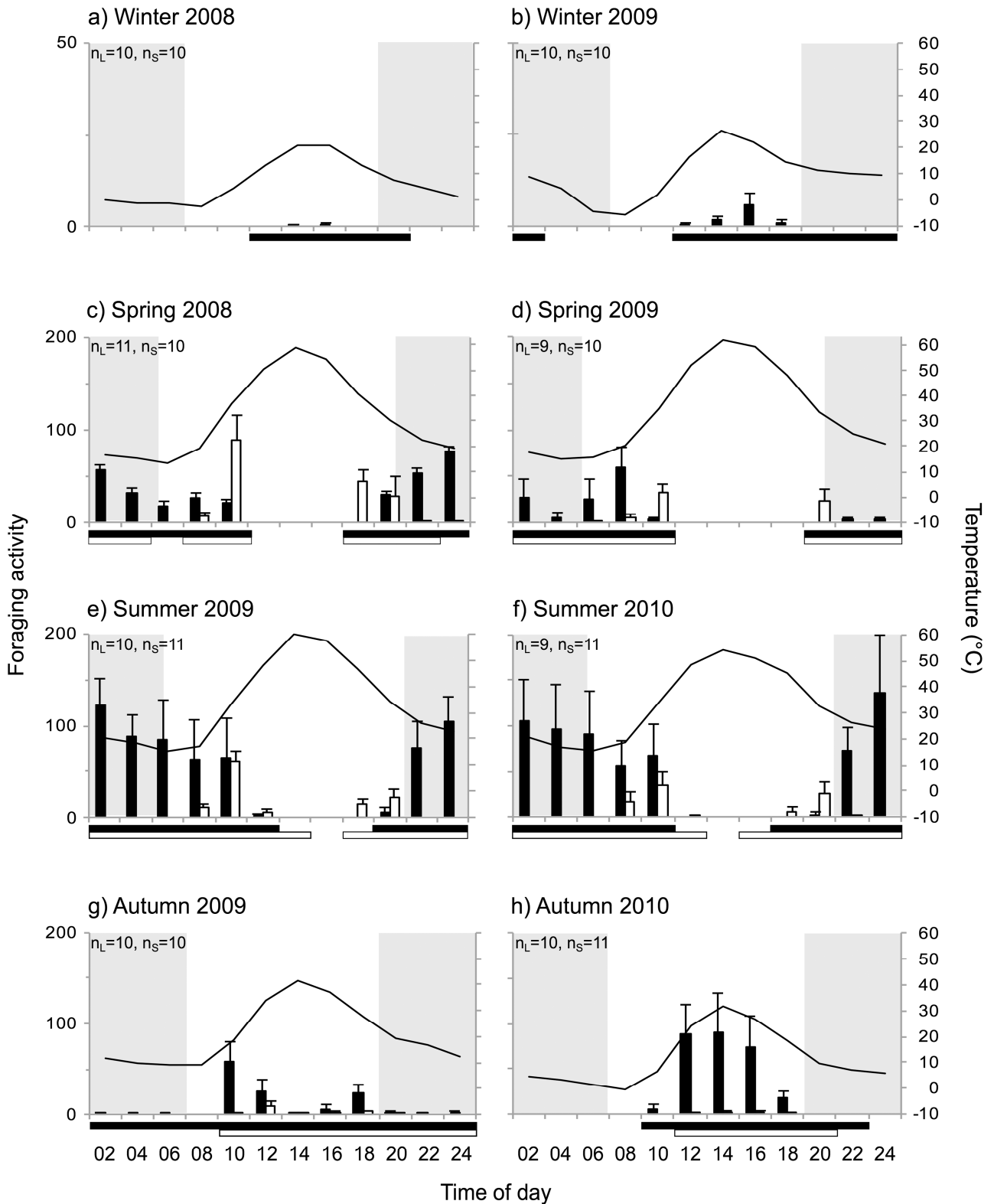
Fig. 2: Foraging activity levels, estimated from the number of loaded workers returning to the nest every five minutes (mean + SE), in *Acromyrmex lobicornis* (black bars) and *A. striatus* (white bars) colonies throughout the day, during winter (a, b), spring (c, d), summer (e, f), and autumn (g, h) 2008 - 2010 in the central Monte desert. Average soil surface temperature measured near the entrance of each colony throughout the day is also shown (black line). Note that the scale of the activity axis is different for winter subfigures. The number of *A. lobicornis* (n_L) and *A. striatus* (n_S) colonies sampled is indicated for each sampling bout. Horizontal lines show the time of the day when workers perform nest maintenance tasks out of the *A. lobicornis* (black lines) and *A. striatus* (white lines) sampled colonies. Shaded areas indicate nighttime.
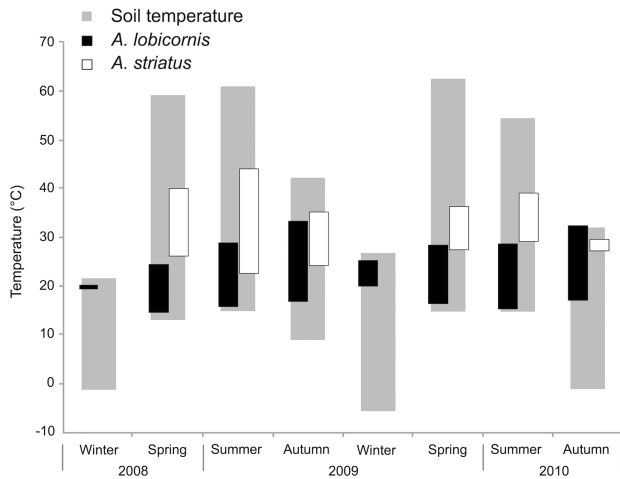
Fig. 3: Average range of soil temperatures at which *Acromyrmex lobicornis* (black boxes) and *A. striatus* (white boxes) colonies were active during each sampling season in the central Monte desert. Grey boxes represent the average range of soil surface temperature measured close to the nests throughout the sampled days in each season.
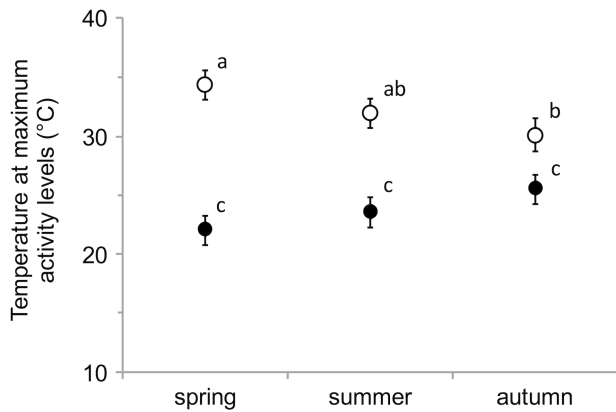

Fig. 4: Temperature of maximum activity (mean ± SE) for *Acromyrmex lobicornis* (black circles) and *A. striatus* (white circles) colonies during spring, summer and autumn in the central Monte desert. Different letters indicate statistically significant differences (Fisher's Least Significant Difference, LSD > 3.58 °C, $p < 0.05$).
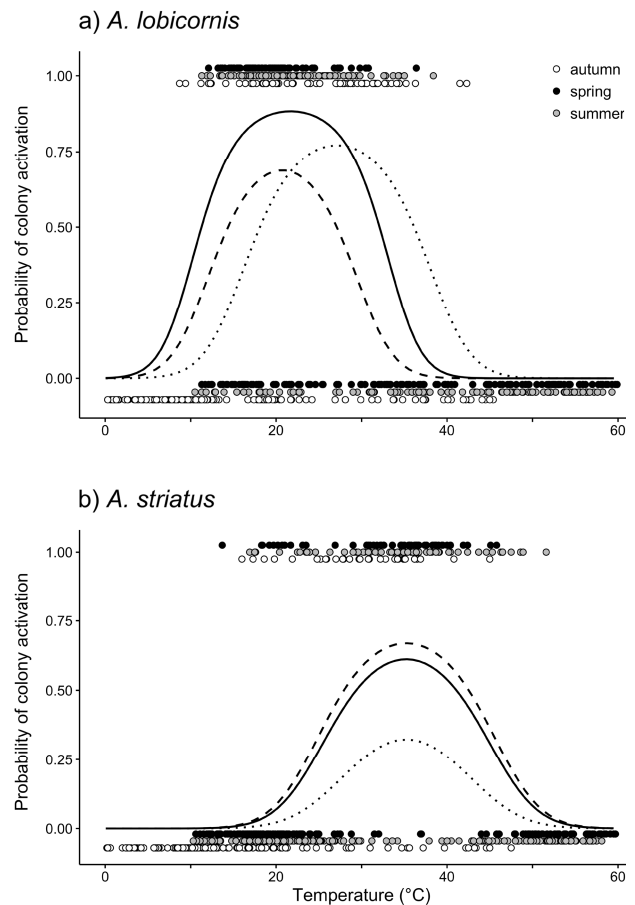

Fig. 5: Predicted probability of colony activation (presence of loaded foragers returning to the nest) for *Acromyrmex lobicornis* (a) and *A. striatus* (b) as a function of soil temperature during summer (full line), spring (dashed line), and autumn (dotted line) in the central Monte desert. Dots show observed data of active (top) and inactive (bottom) colonies sampled in summer (grey dots), spring (black dots) and autumn (white dots) for each species.

ing of *A. striatus* colonies foraging activity in the evenings also coincides with the beginning of *A. lobicornis* foraging (Fig. 2).

Each species foraged within a particular temperature range that was relatively constant throughout the year (Fig. 3). Although both species partially overlapped in their foraging temperature ranges, *Acromyrmex striatus* colonies foraged at higher temperatures than *A. lobicornis* in all seasons (26 - 45 °C vs. 16 - 35 °C, respectively; Fig. 3). Differences in temperature of maximum activity between species varied seasonally ($F_2, 108 = 4.51$, $p = 0.013$), but the temperature of maximum activity was always lower for *A. lobicornis* colonies than for *A. striatus* colonies (Fig. 4). The temperature of maximum activity in *A. lobicornis* colonies was more similar throughout the seasons than for *A. striatus* colonies, which showed a slightly lower maximum activity temperature in autumn than in spring (Fig. 4).

The best statistical models to predict the foraging state of *Acromyrmex lobicornis* colonies included season, soil temperature (in its linear and quadratic form), and the Season × Temperature[2] interaction as fixed factors (difference with additive model: $\chi^2_2 = 39.33$, $p < 0.001$). The inclusion of the Season × Temperature (linear form) term was not justified by model fit ($\chi^2_2 = 2.30$, $p = 0.316$). The best model for *A. striatus* colonies included only season and soil temperature (in its linear and quadratic form) as fixed factors (difference with additive model: $\chi^2_2 = 6.24$, $p = 0.044$). The inclusion of either interaction terms did not significantly increase the model fit (including Season × Temperature: $\chi^2_2 = 1.08$, $p = 0.582$; including Season × Temperature[2]: $\chi^2_2 = 1.36$, $p = 0.507$). Goodness of fit of the chosen model was higher for *A. lobicornis* than for *A. striatus* ($R^2 = 0.45$ and 0.27, respectively). *Acromyrmex striatus* colonies showed low probabilities of being active during autumn (< 40%) and high probabilities (> 60%) around 35 °C in spring and summer, while *A. lobicornis* colonies were active preferentially at 10 - 30 °C in spring and summer and at 20 - 35 °C during autumn (Fig. 5).

The best model to predict the mean foraging intensity of *Acromyrmex lobicornis* colonies included soil tempera-
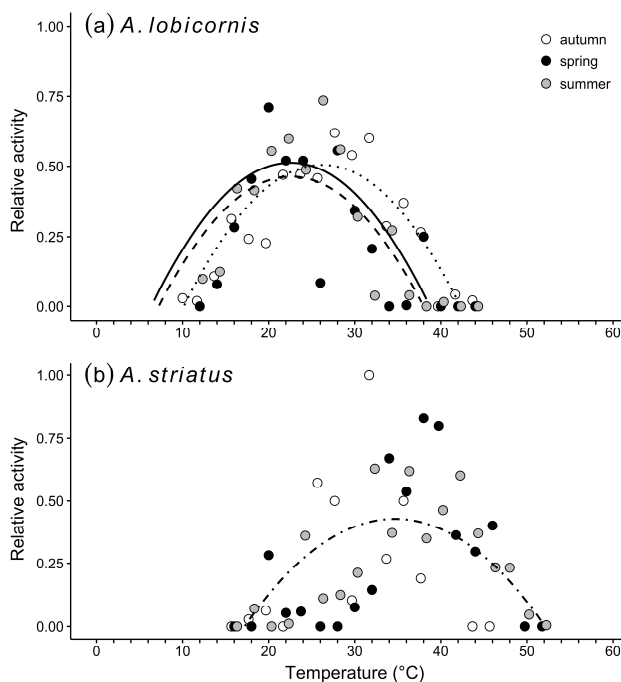
Fig. 6: Mean relative activity levels (proportion of active foragers) of *Acromyrmex lobicornis* (a) and *A. striatus* (b) colonies as a function of soil temperature in spring (black dots), summer (grey dots), and autumn (white dots) in the central Monte desert. Lines represent best fitting model predictions for *A. lobicornis* in summer (full line), spring (dashed line), and autumn (dotted line), and in the three seasons for *A. striatus* (dash-dotted line).

ture (in its linear and quadratic forms), season, and the interaction Temperature × Season. We had statistical evidence to include the interaction term Season × Temperature ($\chi^2_2 = 14.15$, $p < 0.001$); however, the inclusion of the other interaction term Season × Temperature^2 was not justified by model fit ($\chi^2_2 = 1.26$, $p = 0.532$). For *A. striatus* colonies, the best model describing the variation in foraging intensity included only soil temperature as linear and quadratic terms. The inclusion of Season as a factor was not supported by the model fit ($\chi^2_2 = 1.52$, $p = 0.466$), but we had statistical evidence to include the quadratic term for soil temperature ($\chi^2_2 = 57.49$, $p < 0.001$). Goodness of fit of the chosen model was slightly higher for *A. lobicornis* than for *A. striatus* ($R^2 = 0.28$ and 0.24, respectively). Foraging intensity showed a pattern similar to colony activation: the model predicted maximum activity for *A. striatus* colonies at 36 °C, whereas, for *A. lobicornis*, it was expected at 24 °C in spring and summer and 28 °C during autumn (Fig. 6).

Discussion

Our study shows that temperature is an important factor affecting *Acromyrmex lobicornis* and *A. striatus* foraging patterns. Temperature determines both the timing of colony activation and the external activity levels of the colonies. These two descriptors of foraging activity responded similarly to changes in soil temperature, showing consistent patterns: Both the probability of a colony being active and the number of workers foraging are highest around 32 - 40 °C for *A. striatus* colonies, and around 25 - 28 °C

for *A. lobicornis*, with slight variations among seasons. We also documented distinct daily and seasonal activity patterns for both species, as expected given the close relationship between temperature and time of day in this ecosystem.

Light or direct radiation and its associated factors (e.g., predator activity) were not an important factor determining these species' external activity. *Acromyrmex lobicornis* forages during the night in summer and spring, and switches to diurnal foraging in autumn, when temperatures are lower. In turn, *A. striatus* changes its pattern from bimodal in spring and summer, with one activity peak during the morning and one in the afternoon, to one single period of low activity concentrated during the hottest part of the day in autumn.

Since ants are ectothermic organisms with small body size, they are particularly vulnerable to heat loss (or gain) when they leave their underground nests (WHITFORD & ETTERSHANK 1975). Thus, during the coldest season in the Monte desert these ants can only forage during midday, when soil temperature is high enough. For *Acromyrmex striatus*, even winter middays at this latitude are presumably not warm enough to maintain significant external activity. During autumn, soil temperature at midday reaches a maximum between 30 and 40 °C (within both species' tolerated ranges). Consequently, we observed continuous activity of both species without a pause during midday. In contrast, during the hottest seasons soil temperature rises considerably around midday (up to 70 °C in our records) until it may become too hot for ant activity or survival. Some ant species can overcome this extreme heat through physiological adaptations, such as higher levels of thermal shock proteins, low cuticular transpiration and low metabolic rates (WEHNER & al. 1992, GEHRING & WEHNER 1995). Other species show behavioral adaptations, such as taking frequent breaks in thermal refuges (MARSH 1985, WEHNER & al. 1992, CERDÁ & RETANA 2000), raising their gaster to protect vital organs from the high soil temperatures (CERDÁ & RETANA 2000, CERDÁ 2001) or adjusting the temporal patterns of external activities (CERDÁ 2001). Under this last strategy, workers restrict themselves to activities inside the nest and stop foraging during the hottest hours of the day. This results in temporal foraging patterns that reveal their thermal preferences. It is usual for species that forage within moderate temperatures to change their activity patterns from diurnal to vespertine or nocturnal in the hotter months (e.g., WHITFORD & ETTERSHANK 1975, GAMBOA 1976, BROWN & al. 1979, MINTZER 1979, MEHLHOP & SCOTT 1983), while thermophiles show bimodal foraging patterns only avoiding the hottest hours of summer middays (e.g., POL & LOPEZ DE CASENAVE 2004, CERDÁ & RETANA 1994, BUCY & BREED 2006). *Acromyrmex lobicornis* and *A. striatus* foraging activity patterns in the Monte desert strongly suggest that they cope with both extremes of unsuitable temperatures of this desert through behavioral adaptation.

Although we detected some variability among seasons, each species showed a specific and distinctive temperature range in which they forage actively. The temperature of maximum foraging intensity is lower for *Acromyrmex lobicornis* than for *A. striatus* colonies. This could explain why we found such a small overlap in these species' daily activity patterns in spring and summer. During the hottest

seasons (when both species have the highest foraging activity), *A. lobicornis* is mainly nocturnal and *A. striatus* is exclusively diurnal, so they only overlap when *A. lobicornis'* activity is ceasing and *A. striatus'* is starting. During autumn, the soil reaches a maximum temperature of ~ 35 °C, which is in the range of tolerated temperatures for both species. Autumn nights and early mornings might be too cold for *A. lobicornis* foragers, so they start foraging during the day and the temporal overlap between the two species increases. Interestingly, *A. striatus* colonies show very scarce activity during autumn (even though the soil temperature reaches their preferred temperature range for several hours). These temporal shifts in activity intensity, as well as the temperature specialization observed in both species suggest that the avoidance of competitive interactions might be another factor affecting these species' foraging patterns.

One expected outcome of temporal niche partitioning among competing species is that the dominant species forage at temperatures perceived as moderate while subordinate species forage at temperatures closer to their tolerance limits (CERDÁ & al. 1997, 2013). *Acromyrmex lobicornis* has some typical characteristics of a dominant species, such as big colonies and mass recruitment (STUBLE & al. 2017), which facilitates resource monopolization when compared with the numerous but relatively modest-sized *A. striatus* colonies in the area (F.A. Milesi & J. Lopez de Casenave, unpubl.). We also observed that in our study site colonies ceasing their activity from one season to the next (presumably because they died or moved) happened more often in *A. striatus* colonies than in *A. lobicornis* colonies, which is consistent with the idea that *A. lobicornis* is the dominant species. If temporal niche partitioning occurs for these two coexisting species, *A. lobicornis* should act as the dominant species forcing *A. striatus* to forage farther from its optimal temperature under limiting resources or constrained conditions. Under this hypothesis, in spring and summer (the seasons when leafcutter activity is the highest) the range of variation in soil temperature throughout the day would allow each species to have enough time to forage within their preferred temperature range, avoiding potential interaction costs derived from overlapping their foraging periods. In autumn, however, the overall lower temperatures would result in a more challenging situation for the subordinate species, with only a few hours a day within its preferred temperature range and the dominant species becoming diurnal. Greater overlap in foraging timing may result in higher costs from interference competition, so responses such as lower general external activity in the subordinate species are to be expected. This kind of response could be somewhere in the range from completely plastic (if it depends on the aggregation of individual ant responses to interference interactions; e.g., SAVOLAINEN & VEPSÄLÄINEN 1989, PAULSON & AKRE 1991) to completely rigid (if it is a fixed behavioral trait resulting from adaptation to competition in the past; YAZDANI & AGARWAL 1997). Comparative studies on the foraging patterns of these two species in sympatry and allopatry and along a south-north gradient of varying thermal regimes would contribute to discerning fixed behavioral traits (and physiological adaptations) from active behavioral avoidance.

Alternatively, the observed segregation could be a simple consequence of this region being a contact area for species adapted to different conditions in their original areas. In fact, although both species have a similar general distribution, *Acromyrmex striatus* is generally restricted to warmer environments, while *A. lobicornis* has proven to be more cold-tolerant by recently extending its range south into Patagonia (FARJI-BRENER & RUGGIERO 1994). Finally, more complex variables that are directly related to temperature (e.g., relative humidity) could be the ultimate drivers of the observed changes in foraging patterns (CALDATO & al. 2016), particularly considering that ants are sensitive to water loss in deserts (HEATWOLE 1996). To evaluate these alternative explanations, the thermal tolerance ranges of these ants at the individual level should be studied, as well as the association between micro-climatic variables and foraging efficiency at the colony level (see, e.g., DREES & al. 2007, JAYATILAKA & al. 2011). This would also determine if their observed temperature range in the central Monte desert is driven by physiological constraints or competitive interactions (i.e., they may tolerate a broader range of environmental conditions, but restrict themselves to a smaller range to avoid aggressive interactions).

Temperature is a major environmental factor in temperate desert habitats that affects the behavior of key organisms and modifies the strength of their direct and indirect interactions. In this study, we found that the foraging activity of *Acromyrmex lobicornis* and *A. striatus* respond to daily and seasonal changes in soil temperature. This study, together with further studies on the response of these ants to temperature, will allow us to predict the effects of expected global temperature rise on leafcutter activity and the consequent changes in their potential impact as herbivores.

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