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Competition between grass-cutting *Atta vollenweideri* ants (Hymenoptera: Formicidae) and domestic cattle (Artiodactyla: Bovidae) in Argentine rangelands

Andrea C. Guillade[1] and Patricia J. Folgarait

Departamento de Ciencia y Tecnología, Universidad Nacional de Quilmes, Roque Sáenz Peña, Bernal 1876, Argentina

Abstract

1 Leafcutter ants are considered the most important herbivores in the Neotropics. *Atta vollenweideri* is a rangeland pest that competes with cattle for grass, reducing the carrying capacity of pastures.

2 However, there is much controversy regarding their degree of herbivory, pest status and competition with cattle. Furthermore, their economic injury level (EIL) has not been determined.

3 We studied *A. vollenweideri* in competition with cattle in a natural pasture in Argentina, quantifying primary productivity, as well as herbivory by ants alone and together with cattle. Productivity and herbivory by ants were contrasted with cattle dietary requirements under two grazing regimes. We estimated the first EIL for leaf-cutting ants in rangelands.

4 Productivity was highly variable throughout the seasons. Competition between ants and cattle was evident during the low productivity periods, with evidence of ants being more affected by cattle unless ants store food during the productivity peak in summer and autumn.

5 The EIL was 0.29 ant nests per hectare, although it likely overestimates the importance of these ants as pests. We discuss the shortcomings of a classic EIL formula for estimating the damage potential of social insects.

Keywords Cows, economic injury level, grass-cutting ants, herbivory, natural pastures.

Introduction

Leaf-cutting ants (Formicidae, Attini) are considered the most successful herbivores in the Neotropics (Weber, 1972; Hölldobler & Wilson, 1990), removing more plant mass than any other animal group, including large mammal herbivores, which are scarce in the New World (Bucher, 1987; McNaughton *et al.*, 1993). Unlike other herbivores that utilize foliage directly for nutrition, higher Attines depend exclusively upon freshly harvested vegetation as a substrate for their fungal garden (Fowler, 1983). Mature colonies contain over a million workers and harvest many kilograms of plant material per year, and this great requirement for vegetation often puts them in conflict with human interests, with several crops grown in the Neotropics and subtropics being attacked by leaf-cutting ants (Cherret & Peregrine, 1976; Della Lucia, 1993; Boaretto & Forti, 1997; Cantarelli *et al.*, 2008; Montoya-Lerma *et al.*, 2012). As a result, ants in the genus *Atta* Fabricius have been regarded as pests from as long ago as the 19th Century (Cherret, 1986).

Certain *Atta* species, including *Atta capiguara* Gonçalves and *Atta vollenweideri* Forel, specialize in cutting monocotyledon grasses, which puts them in direct competition with cattle in pastures (Robinson & Fowler, 1982). Moreover, according to Fowler and Saes (1986), the impact of these ants on cattle production is not limited to grass consumption alone. The physical space occupied by nests and foraging trails reduces the area that grass can grow on, decreasing the carrying capacity of the land. Cattle grazing is also affected by foraging ants as a result of direct attack from ants, as well as injury from the ants' thoracic spines when they are accidentally consumed by cows (Fowler & Saes, 1986).

Correspondence: Andrea C. Guillade. Tel.: +54 11 4365 7100 (ext 5810); fax: +54 11 4365 7182; e-mail: andreaguillade@gmail.com

[1]Present address: Laboratorio de Hormigas, Departamento de Ciencia y Tecnología, Universidad Nacional de Quilmes, Roque Sáenz Peña 352, Bernal 1876, Buenos Aires, Argentina.

There is great variation in the calculations of the amount of grass consumed by ants and their perceived consequences to cattle production. Through exclusion experiments, Robinson and Fowler (1982) estimated a yearly intake of 231.5 kg dry weight/nest/year, which, at a density of 4 nests/ha for *A. vollenweideri*, amounted to 972.5 kg/ha/year. According to their study, this was twice the intake by cows, although the density at which cattle were present was never stated. Similarly, primary productivity was not clearly reported, and it was stated that their results in this area were not statistically significant. They also calculated yearly intake of grass by an *A. vollenweideri* colony at 217.75 kg dry weight/ha/year, although this value was obtained by measuring grass intake of a colony on a single summer day and then considering shifts in diel foraging rhythm. The method by which they arrived at their final value is unclear and it is unlikely to reflect the complexity of shifts in foraging rhythms exhibited by these ants. In a previous study, Jonkman (1980) criticized estimations of herbivory obtained through such means. By weighing the contents of living fungal chambers and refuse chambers, and then applying a 'conversion factor', he calculated yearly intake of grass by an adult *A. vollenweideri* colony to be 36 kg dry weight/ha/year. He then estimated the primary productivity necessary to sustain cattle at a density of 0.4 cows/ha, which was 730 kg dry weight/ha/year; therefore, according to his results, one *A. vollenweideri* colony would consume approximately 5% of the grass needed to sustain one cow. These results are also questionable because the conversion factor is not explained, and the measures were obtained from a single colony. We did not find any other published data regarding this matter.

Argentina is the fifth largest producer of cattle and the seventh most important beef/cattle exporting country in the world, with Santa Fe province in the Chaco eco-region containing 27% of the national stock, with a mean stocking density of 0.93 cows/ha (Chiossone, 2006). *Atta vollenweideri* is regarded as a pest and a cow competitor because it is one of the dominant native herbivores in this phytogeographic region (Bucher, 1987). Its nests are mostly found on heavy clay soils, and it feeds mainly on native monocotyledons of high forage value for cattle (Chiossone, 2006). Despite its perceived economic importance, there are no reliable quantifications of the pest status of this ant, nor its herbivory or competition with cattle, for any region in Argentina. More significantly, an evaluation of the economic injury level (EIL) has not been conducted for any leaf-cutter ant species within rangelands in this or any other region.

The EIL determines the point in agricultural production systems where pest management costs are equal to the benefits from the control action. Thus, ant population levels below the EIL are not economically profitable to control (Pedigo *et al.*, 1986). Unfortunately, EILs have often been the weakest components in rangeland management (Poston *et al.*, 1983). Consequently, there are no best-practice methods for *Atta* control and, instead, cattle ranchers use their own criteria based purely on personal opinion. In the present study, we provide an accurate assessment of the consumption of standing biomass by ants, with and without competition with cattle, aiming to establish an EIL for *A. vollenweideri* in natural pastures.

Materials and methods

Study site

The study was conducted from September 2010 to October 2011 in natural pastures located at Tierra Buena cattle ranch in San Cristobal, Santa Fe province (30°12′S, 61°09′W), in the Chaco phytogeographical province in Argentina. The herbaceous stratum was mainly composed of *Stypa* spp., *Bromus* spp, *Setaria* spp, *Botriochloa laguroides*, *Paspalum urbillei*, *Paspalum dilatatum* and *Chloris* spp. (Cabrera & Willink, 1973).

Monthly production of grass in presence and absence of herbivores

We chose three areas of natural pastures, each with a cattle density of 1 cow/ha, which is considered to be the sustainable carrying capacity in this area (Chiossone, 2006). Each area was fenced, with a surface of at least 25 ha, and was separated from the others by at least 500 m. Within each area, we selected a 1-ha plot containing a single *A. vollenweideri* nest of similar height (mean = 0.52 m), diameter (mean = 5.6 m) and number of active trails (mean = 11 trails per nest), and we also ensured that no other nests of *Atta* or any other leaf-cutting ant species were present within the plots, nor were there any foraging trails from ants in neighbouring areas. Therefore, the density of *A. vollenweideri* nests at each plot was of 1 nest/ha. Within a 50-m radius of the nest, where ants were actively cutting grass, we placed six sets of four treatment quadrats, comprising two types of exclosure cages 25 × 25 × 20 cm (width, depth, height) and an open grazing area. Exclosure 1, no herbivores (NH): the cage comprised fine wire mesh (0.2-mm opening) on all sides over a wire (diameter 5 mm) frame, buried 5 cm into the soil, preventing herbivore access. Two of these exclosures were used per set. Exclosure 2, ants only (AO): the cage comprised hexagonal wire mesh (10-mm opening) over a wire (diameter 5 mm) frame, buried 5 cm into the soil, which allowed ants to enter into the exclosure but excluded cattle grazing. Observations made prior to commencing the experiments confirmed that ants could enter these exclosures and cut and carry plant material from them. Open grazing area, ants plus cattle (A + C), comprised a 25 × 25 cm area with corners marked using metal stakes, in which ants could harvest grass and cattle could graze unimpeded.

Quadrats of each set were positioned 25 cm apart from each other to minimize the impact of any possible differences in microhabitat and sets were placed at least 20 m apart.

Grass was cut from both NH cages on every sampling date, with one cage remaining on the same location throughout the study (NH), and the other (NHm) being moved to a different location (25–50 cm from the first NH cage) each sample time. The NHm cage allowed us to test whether there was an effect in plant productivity from the subsequent cuttings on the same location (NH) compared with cuttings (simulating grazing) in different places throughout the year (NHm). Both NH cages and the AO cage were covered with thorny branches to discourage cattle interference; these branches were not sufficiently thick to shade the cages and affect grass productivity.

It was not possible to enclose plots and remove all leaf-cutting ant nests from them to evaluate only cattle grazing per plot. Grass production available to cattle was therefore calculated as the difference between standing crop in AO and A + C cages and, accordingly, it was not included in the statistical analyses.

Sampling was conducted monthly, with the exception of January and July 2011. Sampling involved cutting all plant material within each quadrat to 1 cm above the ground. The plant material was dried at 60 °C for 72 h, and weighed using a V200 (Acculab, U.K.) precision digital scale (accuracy of ± 0.01 g).

Impact of ant activity on pasture availability for cattle

To determine whether the presence of ants at a density of 1 nest/ha affected the capacity of the pasture to sustain cattle at 1 cow/ha, we calculated the minimum grass production necessary for two types of management regimes typical of the region, both with a density of 1 cow/ha. Management regime 1 (M1) involved a hypothetical herd with bulls kept together with cows at all times, which results in calving in all seasons. Calves are kept with the herd after weaning. Monthly production required was estimated by averaging the dietary requirements of cattle of all age groups, with all ages equally represented each month (Carrillo, 1993). Management regime 2 (M2) had bulls separated from the herd until breeding time from October to December, with calving from July to September, and weaning in February (Carrillo, 1993). Thus, cattle at different ages are found in varying proportions throughout the year. In January and February, the herd consists mainly of pregnant cows, lactating cows and steers; from March to September, it comprises cows regaining weight after weaning, pregnant cows, weaned calves and steers. Finally, from October to December, it comprises bulls, pregnant cows, lactating cows and steers. Required production was calculated using the combinations of cows for each period. The grass requirements for a third regime was calculated, whereby weaned calves and steers were kept apart from the herd. However, the difference between the amount of grass required in this regime and M2 was negligible and so M2 may apply to both management regimes. The grass requirements under these regimes was compared with the quantified production in each plot after ants had fed (AO), as well as with consumption by ants, calculated as NH − AO.

EIL

The EIL, defined as the density of nests per hectare resulting in a loss of production equaling the cost of control (Peterson & Hunt, 2003), was calculated using the formula $\text{EIL} = C/VD'K$ (Pedigo *et al.*, 1986), where C is the cost of control per production unit (US$/ha), calculated as the cost of insecticide per hectare + the cost of application. We calculated the EIL using fipronil because this is the most effective pesticide against *Atta vollenweideri* (Guillade & Folgarait, 2014). Considering that the market value of fipronil is US$1500/L (Bayer Crop Sciences, 2013), 20 mL of fipronil is sufficient to exert control over one *A. vollenweideri* nest (Guillade & Folgarait, 2014), and that the density of ants was 1 nest/ha, we estimated the cost of pesticide at US$30/ha. We added to this the cost of man hours and equipment (US$24), considering the possibility of having to repeat the treatment after 6 months. The market value (V) of the final product was US$2.5/kg (Mercado de Liniers, 2013). D' is the calculated loss of production (kg/steer) per ant nest. This measurement was based on a steer needing to consume 15 kg dry weight of grass to gain 1 kg (Carrillo, 1993) and the calculated mean percentage of the total primary production of grass consumed by one nest (see Results). We also included in D' the loss of productivity as a result of the physical space occupied by a nest and its foraging trails. The size of 32 mature *A. vollenweideri* nests measured in six 25-ha areas of natural pastures at Tierra Buena ranch in 2009 had a mean diameter of 5.4 m and the mean number of trails (active and inactive) per nest was 18 (A. C. Guillade and P. J. Folgarait, unpublished data). Considering that the mean length of a trail is 150 m (Röschard & Roces, 2003) and that its width decreases continually as it branches, from an average 14.5 cm near the nest entrance to 1.5 cm near the cutting area (A. C. Guillade, unpublished data), we estimate that the total surface occupied by all the trails of a nest is 21.6 m^2. If we add to this the 24.54 m^2 covered by the nest itself, the total surface of soil occupied by a nest is 46.14 m^2. Finally, K is the reduction in pest attack, as a percentage converted to proportion, taking values between 0 (non-effective) and 1, which can also be interpreted as the control efficacy by the pesticide (Peterson & Hunt, 2003); K was considered to be 0.9 because a previous study showed 90% effectiveness for fipronil treatments on *A. vollenweideri* nests (Guillade & Folgarait, 2014).

Statistical analysis

After applying the transformation $f(x) = \ln(x + 1)$, data from all three plots were adjusted to a normal distribution according to the Shapiro–Wilk test, with the exception of May, June and August 2011. Levene's test revealed homogeneity of variances for all sampling months except May 2011. Given that the repeated measures analysis of variance (ANOVA) is a potent test even when data are not normally distributed, and only one sampling date did not fulfill the homogeneity of variances assumption, we decided to run this test with all plots together to obtain a general pattern of productivity and herbivory. Furthermore, whenever the assumption of sphericity could not be met, we reported a corrected F (F_C), using the Greenhouse–Geisser correction to adjust the degrees of freedom. We first ran a repeated-measures ANOVA for one factor (NH; HNm) and found no significant difference between primary productivity in NHm cages that were moved after cutting the grass and those NH that remained on the same location throughout the year, in any of the plots and sampling dates ($F_{34} = 0.8$, $P > 0.01$). Therefore, because productivity was not affected by successive cuttings, we used the data from NH cages that were not moved for all further analyses. Second, we performed a one-factor ANOVA (factor: treatment, with three levels, NH, AO and A + C; $n = 18$ for each treatment) with repeated measures to analyze production in the exclosures and quadrats, using as much information as we were able to collect. Afterwards, we conducted an ANOVA for each sampling date to determine on which occasions the differences between treatments were significant, applying the Bonferroni correction for multiple comparisons. Data were analyzed using SYSTAT, version 13 (SYSTAT Inc., 2009).

Results

Monthly production of grass in presence and absence of herbivores

When considering all plots together, mean production in NH cages was 4913 ± 627 kg/ha/year (Table 1). Production in AO cages was 3696 ± 224 kg/ha/year, meaning that ants consumed 1216 ± 871 kg/colony/year. Mean production in A + C cages was 3164 ± 279 kg/ha/year; therefore, when both herbivores were together, they consumed 1749 ± 878 kg/ha/year.

Both production and herbivory varied through time (Fig. 1). Repeated-measures ANOVA showed a significant effect of time ($F_{C5.6} = 105.97$, $P < 0.000$), although no interaction between time and treatment was found ($F_{C11.21} = 0.628$, $P = 0.8$). ANOVAS carried out to compare treatments in each sampling month showed that there were no significant differences between treatments on October 2010 ($F_{2,51} = 1.05$, $P = 0.35$), December 2010 ($F_{2,51} = 2.84$, $P = 0.06$), February 2011 ($F_{2,51} = 0.4$, $P = 0.67$), March 2011 ($F_{2,51} = 2.01$, $P = 0.14$) and June 2011 ($F_{2,51} = 2.23$, $P = 0.11$). On the other hand, we found significant differences across treatments in November 2010 ($F_{2,51} = 6.83$, $P < 0.01$), April 2011 ($F_{2,51} = 5.43$, $P < 0.01$), May 2011 ($F_{2,51} = 6.56$, $P < 0.01$), August 2011 ($F_{2,51} = 3.6$, $P = 0.03$), September 2011 ($F_{2,51} = 5.73$, $P < 0.01$) and October 2011 ($F_{2,51} = 10.07$, $P < 0.01$), with *a posteriori* contrasts showing that there were significant differences between the NH and the A + C treatment (in all cases $P < 0.016$), whereas the AO treatment showed no significant differences compared with the other two (in all cases $P < 0.016$), with the exception of October 2011, when production in AO cages was significantly lower than that in NH cages.

Impact of ant activity on pasture availability for cattle

Yearly consumption by cattle was calculated to be 3.003 kg dry weight/ha/year for M1 and 2.976 kg dry weight/ha/year for M2.

Productivity surpassed the minimum required by both management regimes in spring (October 2010, November 2010 and October 2011) and autumn (March and April 2011), although it was below the minimum required in summer (December 2010) and winter (May, June and August 2011). Productivity was equal to the minimum requirement in two sampling dates, February and September 2011 (Fig. 2). In the only sampling date when productivity was significantly reduced by the presence of ants (October 2011), it was still above the minimum requirement for both management regimes. Peaks of ant harvesting coincided with grass productivity peaks in autumn and spring, with ant harvesting in March, April and October 2011 exceeding (or being equivalent to) cattle requirements under both management regimes.

EIL

On average, one *A. vollenweideri* colony consumed 1216.96 kg dry weight of grass in a year. Given that a steer gains 1 kg for every 15 kg of dry weight grass consumed, the loss of 1216.96 kg of grass to consumption by ants would result in a loss of 81.13 kg steer/nest/year. The loss of productivity through physical space occupied by the ants equals 26.41 kg dry weight grass/year, which translates into a loss of 1.76 kg steer/nest/year. Therefore, D' is 82.89. Using the EIL formula, the EIL = 0.289 nests/ha.

Discussion

The results of the present study provide valuable information on the productivity of natural pastures and leafcutter ant herbivory in the Chaco province. Our data also show seasons when ants and cattle coexist without competing with each other, and represent the first estimation of an EIL for leafcutter ants in rangelands.

The main cause for ants being considered rangeland pests resides in nests being assumed to reduce the carrying capacity for herds. Our comparisons with estimated requirements of cattle under different management regimes show that this concern is not completely warranted at a density of 1 nest/ha and a carrying capacity of 1 cow/ha, which is the mean cattle density for the region studied (Chiossone, 2006). We found, for all three plots, that pasture productivity surpassed the requirements of herds under both management regimes in spring (October) and autumn (March and April), whereas, in summer (November to February) and winter (June to August), it was either equal or less than these minimum levels (Fig. 2).

Grass consumption in the presence of both herbivores was never significantly greater than grass consumption in cages with access to ants only, which indicates a strong competition interaction between both herbivores. Unfortunately, our design prevents us from discriminating with certainty which herbivore was more affected by the interaction because we do not have an independent measurement of cattle consumption alone. Fowler and Saes (1986) determined that the physical presence of ants in the pastures deterred cows from grazing, which, according to them, is a consequence of physical defences by the ants, such as thoracic spines. However, Tadey and Farji-Brener (2007) provided evidence of competition negatively affecting ants as a result of other reasons (see below). Ants have been considered competitors against cattle for grass (Robinson & Fowler, 1982; Fowler & Saes, 1986) and the present study showed that, at a density of 1 nest/ha, this competition appeared to affect ants more negatively than it did to cattle. This was particularly evident in Plot 3, where grass yield was 22% less than in the other two plots: this reduction in productivity translated into an 87% reduction in consumption by ants, whereas consumption by ants plus cattle decreased by only 25%, and, in those instances, production was still sufficient to meet the minimum required by cattle under both management regimes (3003 and 2976 kg/cow/year, respectively). Two hypotheses can explain these results. First, when grass production became a limiting factor, it appeared that the ants were displaced in the competition with cattle, presumably to less palatable food sources. The negative effects of this interaction have been previously reported by Tadey and Farji-Brener (2007) in the Monte desert in Argentina (for vegetation composition, see Cabrera & Willink, 1973) for *Acromyrmex lobicornis*. It was noted that grazing by cattle reduced plant richness and cover, thus affecting ant diet, which was demonstrated by a reduction in nutrient quality in their refuse dumps. These dumps act as nutrient hotspots, which were considered relevant to wood succession in the Paraguayan Chaco (Jonkman, 1976) and their importance as a source of soil fertility has proven

Table 1 Mean ± SD production in no herbivores (NH) ($n = 6$), ants only (AO) ($n = 6$) and ants plus cattle (A + C) ($n = 6$) cages per plot

Plot	Production in NH cages	Production in AO cages	Consumption by ants	Production in A + C cages	Consumption by ants + cattle
Plot 1	5136.66 ± 673.50	3269.33 ± 294.81	1867.33	2638.00 ± 489.42	2498.66
Plot 2	5499.50 ± 1457.25	3939.50 ± 1208.95	1560.00	3637.50 ± 768.66	1862.00
Plot 3	4104.56 ± 1149.16	3881.00 ± 773.47	223.56	3216.67 ± 581.10	887.89
All plots	4913.57 ± 627.08	3696.61 ± 224.90	1216.96	3164.05 ± 279.23	1749.52

Consumption by ants only and ants + cattle is calculated as the difference between production in NH cages and AO or A + C cages, respectively.

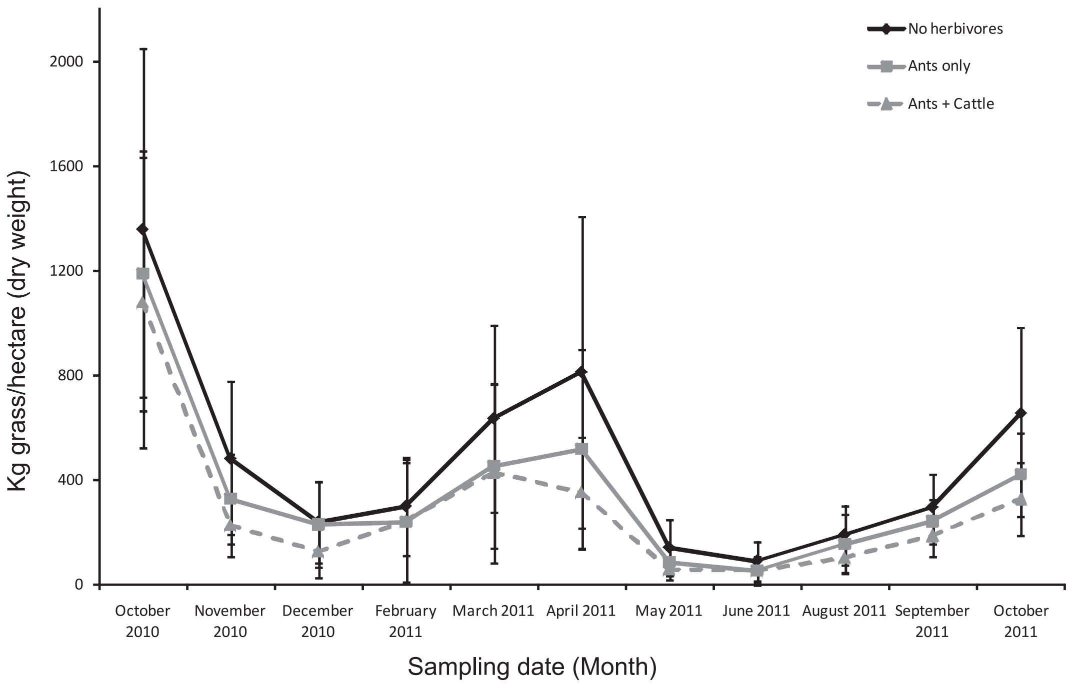

Figure 1 Mean ± SD monthly grass production in the absence of herbivores, in the presence of ants only and ants + cattle treatments.

significant for other environments in Argentina (Farji-Brener & Ghermandi, 2008). Second, an additional interpretation is that ants are accumulating food (cache) for the summer and winter, when the abiotic conditions are worse for ectotherms than for homeotherms, considering that the ants consumed more in the autumn and spring (41.47% and 47.9% of the total annual intake, respectively) than in summer and winter (5.25% and 5.37% of the total annual intake, respectively), whereas cattle kept their feeding rate approximately constant (Fig. 2).

Herbivory by *A. vollenweideri* in the study site was far greater than that reported in studies in the Paraguayan Wet Chaco, although the differences in climatic conditions, vegetation and soil composition between that province and the dry Chaco phytogeographic province in Argentina render these comparisons questionable. In all three plots in the present study, the yearly primary production was such that, even with ants foraging, the surplus during the high-productivity months was sufficient for ants to accumulate food (cache) for the less productive seasons. We recorded two pronounced peaks in productivity during spring and autumn (Fig. 1); ants harvested much of this surplus in productivity, although they still left a sufficient amount for cattle to graze. This cache of plant material, stored in underground chambers to later process in their fungus gardens, is likely what sustained them during the low productivity months, when their intake of plant material was very low (Fig. 2). Cattle, on the other hand, needed to be provided with supplemental forage at critical times (see ideal dietary requirements of cattle and compare with production in A + O cages). Ranchers should be aware that they could harvest the spring and autumn surplus to store forage to give the cattle during summer and winter. This action could control the ant population by limiting their food intake at critical months, and thus preventing them from achieving pest status, unless they move to neighbouring plots if palatable crops are being grown nearby.

We calculated our EIL using the mean consumption by ants obtained from the three experimental plots. However, as shown in Table 1, the consumption of grass by ants in plot 3 was 87% lower than in plots 1 and 2. If the EIL is calculated using the information obtained from plot 1, the result is 0.19 nests/ha but, if the information from plot 3 is used, the EIL is 1.68 nests/ha. However, this last case represents an unlikely scenario for natural pastures because we have never encountered such a density of *A. vollenweideri* nests in the area. We did not need to remove *A. vollenweideri* nests from our plots to keep their density at 1 nest/ha; instead, only two nests of *Acromyrmex heyeri* were removed from plot 1 and one of *A. lobicornis* was

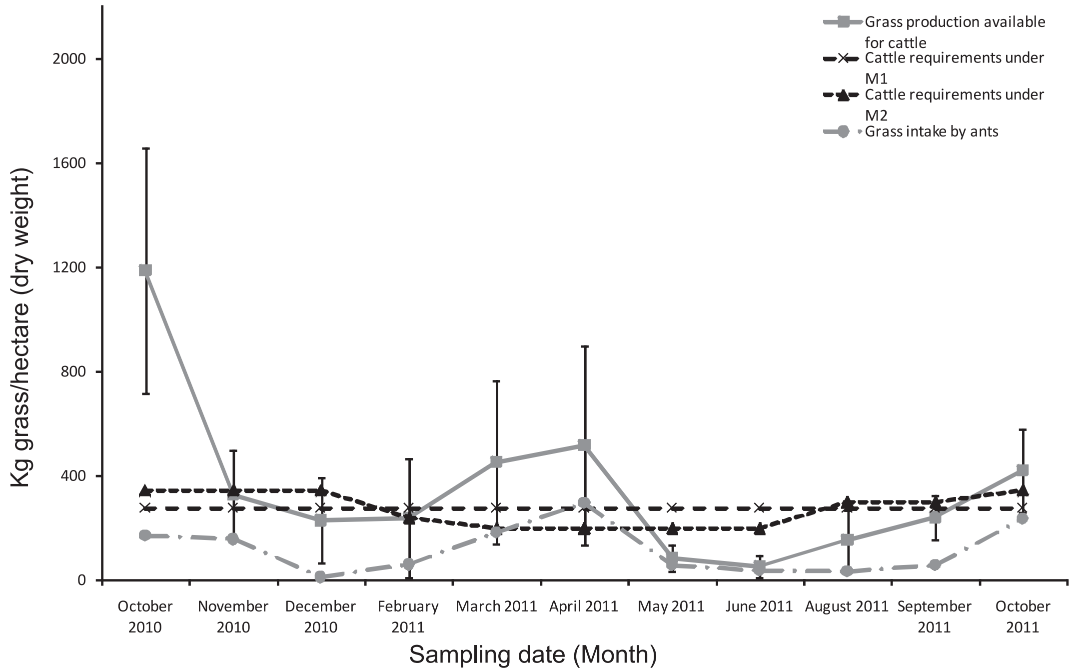

Figure 2 Mean ± SD grass productivity available for cattle after ant herbivory and grass intake by ants, compared with the minimum feeding requirement of cattle at a density of 1 cow/ha, under two grazing situations, management regimes M1 and M2 (for further details, see text).

removed from plot 2. We measured the density of *A. vollenweideri* in neighbouring ranches with similar management and found a mean density of 1.1 nests/ha (A. C. Guillade, unpublished data). Furthermore, in the Paraguayan Chaco, Jonkman (1979) recorded a mean of 0.4 nests/ha for *A. vollenweideri*. This suggests that we are observing the consequences of competition among ants, which has resulted in their present density. If we consider that one nest consumes 1220 kg dry weight grass/year and that one cow needs a 3000 kg dry weight grass/year, then a natural pasture that produces 5200 kg dry weight grass/ha/year could sustain one cow and 1.9 nests, assuming that only *A. vollenweideri* ants are present, that they do not compete amongst colonies, and that two nests consume twice as one nest. Because competition between ants has been widely reported (Parr & Gibb, 2010), it is highly possible that the relationship between ant density and grass consumption is not linear, and therefore the pasture could sustain even more nests without compromising its carrying capacity for cattle. Further research should explore actual consumption of grass by ants at a greater density, which might be possible in sown pastures, or in places where only *Acromyrmex* species are present, to determine the nature of the relationship between ant density and grass consumption.

Importantly, the formula used to calculate the EIL might be leading to an overestimation of the critical nest density for *A. vollenweideri* in natural pastures, for two main reasons. First, the numerator in the equation should ideally contain the ecological cost of control, a term estimating the cost to the environment resulting from the use of the pesticide in question (Higley & Wintersteen, 1992). Although application of fipronil with backpack insuflators can be conducted at each nest, the mist generated can easily affect nontarget organisms. It is also a common practice to spray this pesticide along the perimeter of each grazing plot, instead of on the nests. Unfortunately, we do not possess the data necessary to estimate the ecological cost of control; however, chemical control is likely to result in the loss of many ecological services (Guillade & Folgarait, 2014). Second, the assumption of a linear relationship between grass consumed and weight gained by steers, although necessary for the purposes of calculating the EIL, is a simplification that is likely overestimating the value of the primary production in the pasture because the weight gained by steers is also dependent on several dietary supplements throughout breeding (Carrillo, 1993). As it stands, the information required for a more conservative version of the formula, such as the injury unit per pest (Peterson & Hunt, 2003), is not available for leafcutter ants in pastures, and obtaining it by extrapolation of data collected for other nonsocial species or crops would lead to unreliable results. These points enforce the need for extensive research on the impact of ant activity on various agro-ecosystems, as well as the development of a formula to calculate EIL that takes into account the particularities of dealing with social insects in very long-lived, largely sessile colonies, and with very peculiar patterns of population growth and dispersal (Hölldobler & Wilson, 1990; Parr & Gibb, 2010). Nonetheless, we consider that, at a density of one nest every 3 ha (EIL = 0.29), the activity of ants would certainly not affect cattle rearing, and would help conserve the beneficial effects of these insects on the rangeland (Folgarait, 1998; Montoya-Lerma *et al.*, 2012).

In conclusion, our research shows that, despite biased perceptions, leafcutter ants in natural pastures are not necessarily pests, and that an assessment of pasture productivity and herbivory using exclosures can help improve range management strategies, reducing the costs of production through the elimination of unnecessary pesticide applications. Although estimations of herbivory and pest potential are most reliable for the region in which they are conducted (Fowler & Saes, 1986), our results may be used as a guideline for cattle ranchers exploiting similar landscapes. Further studies are urgently needed to assess the herbivory and pest status of other leaf-cutting ant species in different crops, as well as forestry, to establish EILs for different species and situations. This should lead to a rationalization in the control of these insects, using objective ecological tools to improve the decision-making process, instead of relying on subjective perceptions.

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