Behavioural flexibility does not prevent numerical declines of harvester ants under intense livestock grazing

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Abstract. 1. Human-induced rapid environmental change may decrease food resources and create unfavourable conditions for native species. Organisms showing a flexible foraging behaviour can exploit novel or alternative foods and are more likely to persist, whereas less flexible organisms might suffer starvation and numerical reductions.

2. This study assessed whether declines in the quality and availability of seeds prompted by grazing provoke behavioural and numerical responses in *Pogonomyrmex mendozanus* ants, and aimed to test whether behavioural flexibility buffers habitat degradation and prevents numerical declines.

3. Heavy grazing caused seed reductions, especially of the highly consumed and preferred grass seeds, and triggered two kinds of ant responses. Ants expanded their diet by incorporating a greater proportion of non-seed items, and they reduced foraging activity. As a consequence, the rate of food intake per colony lessened, particularly that of carbohydrate-rich seeds like grass seeds. Colony density under heavy grazing also fell.

4. Habitat degradation triggered a cascade of mechanisms that starts with a decrease in the seed resources and continues with changes in ant behaviour. However, behavioural responses were insufficient to prevent ant numerical declines. The results of this study suggest that the reduction in the colony density under habitat degradation was provoked by ant nutritional deficit and starvation, and predict a deterioration in body condition, colony performance and reproduction of ants, which deserve further assessment.

Key words. Colony density, expanded diet, foraging, Monte desert, *Pogonomyrmex*.

Introduction

A key issue for disturbance ecology and conservation is to understand and predict which species are able, and which are not, to cope with human-induced rapid environmental change (Sih *et al.*, 2010). Many species are not able to respond and adjust to rapid habitat alteration and are susceptible to population decline and local extinction, whereas others are extremely successful under the same circumstances and may become pests (Sih *et al.*, 2010; Wong & Candolin, 2015). When habitat conditions change rapidly, over shorter timescales than a lifetime, phenotypically plastic organisms can show quick and reversible changes in behaviour, physiology or morphology,

which may imply an advantage over stereotyped organisms (Piersma & Drent, 2003; Charmantier *et al.*, 2008; Whitman & Agrawal, 2009). The ability to respond behaviourally to habitat degradation may avoid starvation and mortality, because such responses – which can be developed and learned quickly by most members of a population (Sih *et al.*, 2010; Wright *et al.*, 2010) – buffer organisms against short-term reductions of resource availability (Grémillet & Charmantier, 2010; Sabarros *et al.*, 2012). Species showing a flexible foraging behaviour are thus more likely to persist in a disturbed environment (Kinnison & Hairston, 2007; Møller, 2009), whereas less flexible species are more likely to emigrate or they may suffer numerical reductions or even become locally extinct (Sol *et al.*, 2005).

Grazing by domestic animals is the most globally widespread land use and a major driver of global vegetation change (Díaz *et al.*, 2007). Intense herbivory by domestic livestock has contributed to the decline of some plant (Díaz *et al.*, 2007)

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and insect species (Fleischner, 1994), affecting plant–animal interactions (Vanbergen *et al.*, 2014) and, ultimately, critical ecological processes (Fleischner, 1994; Vázquez & Simberloff, 2004). In the central Monte desert of Argentina, Pol *et al.* (2014) proposed a cascade model based on explicit biological mechanisms to predict the general effect of livestock grazing on seed resources. Under grazing pressure, the model predicted a reduction in the abundance and biomass of the grass species most consumed by livestock, a decrease in the ability of grass to produce seeds, and a reduction of seed availability in the habitat. Predictions were corroborated in a 3-year study over two different localities (Pol *et al.*, 2014). Given that several seed-eating animals in the region consume the seeds of the same grass species as livestock, the model could be extended to predict numerical reductions of seed consumers owing to cattle grazing. However, a question that remains unchallenged, and may affect predictions, is whether the behavioural flexibility of consumers can mitigate habitat degradation and resource depletion, preventing starvation and population reductions.

Among the harvester ant species that occur in the central Monte desert, *Pogonomyrmex mendozanus* (Cuezzo & Claver) has shown some behavioural flexibility in well preserved habitats in response to seasonal and spatial fluctuations of seed availability. Ants were able to change their diet, including suboptimal or alternative food items, when the preferred grass seeds were scarce (Pirk *et al.*, 2009; Pol *et al.*, 2011). Additionally, they could adjust their foraging strategy (e.g. from individual towards group foraging) and regulate their foraging activity level according to seed abundance near the nest (Pol *et al.*, 2015). However, the level of behavioural flexibility triggered by natural fluctuations of resources might not be sufficient to circumvent heavy and continuous grazing, which severely reduces seed availability (Pol *et al.*, 2014). In such cases, a reduction in foraging activity, the amount and quality of food entered into the nest and, ultimately, lower colony density might be foreseen.

Here we assess behavioural and numerical responses of *P. mendozanus* to changes in seed availability in areas subjected to heavy grazing in the central Monte desert. We use an approach intended to verify the depletion of food resources and changes in the foraging behaviour of ants before hypothesising on the effects of habitat deterioration on colony density. The levels of seed resources (size and composition of soil seed bank), ant behavioural responses (foraging behaviour, diet composition, seed selection) and ant numerical responses (colony density) were evaluated simultaneously over 2 years. A usual approach to assess ant performance in perturbed habitats is considering them as pests that increase land degradation through their foraging impact (Wildemuth & Davis, 1931; Sharp & Barr, 1960; Taber, 1998), but here we evaluate the other side of the interaction: the effect of land degradation on ants.

Materials and methods

Study site

The study was carried out in open woodlands of *Prosopis flexuosa* in the Telteca Natural Reserve (32°20′S; 68°00′W), central Monte desert, Mendoza, Argentina. The climate is

arid, warm and seasonal, with mean annual rainfall of 156 mm (1972–2014), widely concentrated in spring and summer (October–March). Topography comprises a north-northwest – south-southeast oriented valley dune system. High and intermediate landscape levels are dominated by shrubs of *Larrea divaricata*, *Tricomaria usillo*, *Bulnesia retama* and *Atriplex lampa* accompanied by small trees (<3 m height) of *P. flexuosa*. Lowlands are generally covered by taller *P. flexuosa* and *Geoffroea decorticans* trees accompanied by most of the plant species found in higher topographic positions. Grass cover is dominated by perennial (*Trichloris crinita*, *Aristida mendocina*, *Panicum urvilleanum*, *Sporobolus rigens*, *Setaria* spp., *Pappophorum* spp.) and annual species (*Bouteloua barbata*, *Bouteloua aristidoides* and *Aristida adsencionis*). Forb cover is usually very low, although highly variable between years, and includes annual and biannual species (*Heliotropium mendocinum*, *Chenopodium* spp., *Gomphrena mendocina*, *Tribulus* spp., *Sphaeralcea* spp.). Local settlers live in homesteads or 'puestos' located in interdune positions and based around hand-dug wells that reach the water table and supply both people and livestock with water. The area around the 'puestos' is more heavily grazed by goats and cattle than is the case in more distant locations.

Sampling design

We assessed behavioural and numerical responses of harvester ants to changes in the size and composition of soil seed banks in two floristically and topographically similar areas which had been subjected to contrasting grazing conditions since the creation of the reserve in 1986. The Jagüel area (32°22′S, 67°58′W) had suffered from intense grazing pressure by cattle, horses and goats, whereas the Llantas area (32°18′S, 67°55′W) had been more lightly grazed. Differences in grazing regimes were recently corroborated by using the proportion of livestock dung deposition as a proxy of current and recent livestock pressures (Pol *et al.*, 2014). On average, the frequency of dung from large livestock (mostly cows but also some horses) was about three times higher under intense grazing pressure (0.46 vs. 0.17), although the frequency of dung from goats showed no differences between conditions (Pol *et al.*, 2014). In addition to high floristic similarity, the cover of several plant strata (e.g. trees, low shrubs and forbs) was also similar between conditions, whereas the cover of grasses and tall shrubs had declined significantly in Jagüel (Pol *et al.*, 2014).

We estimated all variables (see later) simultaneously over 500 ha in Llantas and Jagüel during the activity seasons 2011–2012 and 2012–2013. In order to detect the effect of different levels of resource availability on animal behaviour, we followed ant responses at the end of secondary dispersal of perennial grasses when seed bank size reaches a minimum (spring) as well as when the grasses have reproduced and are dispersing their seeds, which then become more abundant in the soil (summer) (Pol *et al.*, 2010).

Soil seed abundance and composition

Pogonomyrmex mendozanus ants mainly forage on recently produced sound seeds from the soil and, occasionally, from

plant spikes (Pirk & Lopez de Casenave, 2006; Pol *et al.*, 2011). To estimate soil seed bank composition, we collected 120 soil samples in Llantas (60) and Jagüel (60), which were distributed at random over an area of ∼10 ha, following the proportional cover of the main microhabitats in the landscape (Marone & Horno, 1997). We used a cylindrical sampler, 3.2 cm in diameter and 2 cm deep, to collect soil samples which were air-dried and sifted through a 0.27 mm mesh sieve in the laboratory. We discarded the finer fraction (the smallest seeds did not pass the sieve), then washed the coarser fraction in the same sieve under water pressure. The residue on the mesh was dried and searched for seeds under a stereoscopic microscope (Marone & Horno, 1997). We identified seeds to the species or genus level and recorded the number of sound seeds (i.e. those that did not crumble when probed with forceps). We ascribed seeds to one of four plant groups: grasses, forbs, shrubs and other more infrequent seeds (e.g. trees, cacti).

Ant diet and seed selection

We studied both the whole diet and granivorous diet in 10 randomly selected colonies over every condition, located >10 m apart from each other. We collected the items returned to every colony by 40–60 workers for assessing the whole diet. Foragers were captured and placed in a plastic vial, which allowed us to collect food items more easily and ensure that even the smaller items were detected. Every colony was sampled over one or two consecutive days on every sampling occasion. Retrieved items were stored in vials, identified under a stereoscopic microscope and assigned to five main categories: (i) seeds; (ii) flowers and fruits (excluding grass caryopses which were considered as seeds); (iii) plant vegetative structures (non-reproductive structures of plants such as leaves or stem pieces); (iv) invertebrates (either partial or complete arthropods); and (v) other items (e.g. vertebrate faeces, soil fragments). The diversity of items was calculated with the Shannon–Wiener index (H). As the total number of items obtained differed between colonies, we standardised the index values to the same number of items (i.e. rarefied to a minimum number of 40 items), using ECOSIM version 7.0 (Gotelli & Entsminger, 2001). In order to establish the composition of the granivorous diet, seeds were identified at least to the genus level and ascribed to one of the four plant groups referred to earlier. The proportion of each food item per colony was averaged across colonies for every sampling occasion. To explore patterns of seed selection in the field, we established the relation between the relative abundance, expressed as proportions, of the most abundant (>5%) seed species in the soil bank and/or ant diet. Seed selection was determined both graphically and through the 95% confidence interval for the concordance correlation coefficient (Zar, 2010).

Foraging activity and foraging success

We evaluated the foraging activity level in six colonies in every grazing condition, whereas the foraging success was evaluated in seven to 11 colonies in Llantas and seven to 10 colonies in Jagüel. Foraging activity was the number of

workers leaving and returning to the nest during a 5 min period. Measurements were made every hour in two daily sampling occasions: in the morning (08.00–12.00 hours) and afternoon (16.00–20.00 hours), in accordance with the bimodal pattern of foraging activity typical of this species in summer (Pol & Lopez de Casenave, 2004). We considered that a forager worker left or came back to the nest when it abandoned or entered an imaginary circle of ∼30 cm diameter surrounding the nest entrance (Pol & Lopez de Casenave, 2004). We recorded the soil surface temperature every hour in a flat area near the nest entrance to confirm that it did not differ between conditions. We used a digital thermometer (stainless steel sensor probe measurement; range −50 to 150 °C, accuracy ±1 °C) buried a few mm into the soil to prevent any increase in temperature caused by artificial differences in direct solar irradiation. We recorded the number of workers returning to the nest with food during 5 min to determine whether foraging success varied between grazing conditions. Measurements were taken during the peak hours of foraging activity (Pol & Lopez de Casenave, 2004), and foraging success was estimated as the proportion of foragers that returned to the nest with food.

Food intake

The number of food items that foragers entered day^{-1} in a colony was measured by taking into account the foraging activity level, foraging success and diet composition in every sampling occasion ($n = 6$ colonies per condition). We multiplied the mean number of workers returning to the nest per hour, accumulated through the number of hours in which ants were active, by the proportion of workers carrying food, and this figure was multiplied by the proportion of the different food items (i.e. seeds, flowers and fruits, vegetative plant structures, invertebrates and other items) (Smith, 2007).

Colony density

Several lines of evidence suggest that most colonies under heavy as well as light grazing were mature colonies. Domestic grazing is a long-standing activity in Telteca and, although cattle load is not homogeneous in space (i.e. it is usually heavier near the 'puestos'), ant colonies have coexisted with cattle for several decades in the overall area. Further, the number of workers in colonies located under both grazing conditions fluctuate near or over the average number of workers measured for the species on mature colonies (i.e. colonies with alates) at the nearby Reserve of Ñacuñán (Nobúa Behrmann *et al.*, 2010, 2013). Finally, the frequency of colonies with alate individuals under both grazing conditions was very similar (R. G. Pol and L. Marone, unpublished). To determine the density of colonies, we set six plots of 50 × 50 m (0.25 ha) >200 m apart from each other dispersed over an area ∼200 ha in every grazing condition, and we located the 12 plots in areas fairly homogeneous in topography, vegetation and soils. Each plot was gridded (25 subplots, 10 × 10 m each) and the number of colonies was recorded. To increase the probability of detecting colonies, we repeated the censuses twice during the period in which ant foraging activity

was highest. Censuses were carried out on sunny days between February and March 2013. Colonies were marked in the field with flagging tape and mapped using a GPS device.

Data analyses

The general design consisted of comparing different variables between the two contrasting conditions: light (Llantas) and heavy (Jagüel) grazing pressure. We assessed differences in the soil seed abundance of grasses and forbs through one-way ANOVAS. Raw data were log-transformed after being checked graphically (scatterplots of residuals against predicted values; Zar, 2010) in order to corroborate normality of the residuals. We did not employ statistics given the extremely high number of zeros in shrub seed sampling. The proportion of food items in the diet, diet diversity, foraging activity, foraging success, colony food intake and colony density were compared between conditions using the t-test or two-tailed Mann–Whitney test when residuals were not normally distributed.

We compared soil temperature regimens between conditions through a two-way factorial ANOVA (grazing level × hour of the day) and performed Tukey *a posterior* contrasts for every hour if overall significant differences were obtained (Zar, 2010).

To assess the correspondence of seed species availability in the soil and its abundance in ant diet (i.e. seed selection patterns), we used the 95% confidence interval for the concordance correlation coefficient (r_c; Zar, 2010, p. 414). Estimation of two-sided confidence limits was performed using the inverse hyperbolic tangent transformation (or Z-transformation) described in Lin (2000). An interval approaching one indicates that seeds were taken in proportion to their availability, whereas an interval lying far from one indicated selection, either positive (i.e. the proportion of that seed in the diet is higher than in the environment) or negative (i.e. it is lower than in the environment). Seed selection patterns were estimated separately for both grazing conditions across all (four) sampling occasions. All parameters were calculated using the online version of Lin's concordance calculator provided by NIWA (https://www.niwa.co.nz/node/104318/concordance).

Results

Soil seed abundance and composition

Heavy grazing resulted in a significantly smaller total soil seed bank density: on average it was eight times higher in light grazing conditions (range 5–18; Table 1). Seeds of grasses and forbs prevailed in all the soils evaluated (97% and 72% of total seeds in Llantas and Jagüel, respectively). The abundance of grass seeds was consistently and significantly lower under heavy grazing (spring 2011: $F_{1, 118} = 22.15$, $P < 0.001$; summer 2012: $F_{1, 118} = 12.16$, $P = 0.001$; spring 2012: $F_{1, 118} = 21.29$, $P < 0.001$; summer 2013: $F_{1, 118} = 28.26$, $P < 0.001$). Grass seeds were more abundant in Llantas in 22 out of 24 paired comparisons of species between conditions (i.e. six species × two sampling occasions × 2 years = 24 contrasts; Table 1). Forb seeds, in turn, also suffered reductions but they were less

consistent (spring 2011: $F_{1, 118} = 4.7$, $P = 0.03$; summer 2012: $F_{1, 118} = 2.15$, $P = 0.15$; spring 2012: $F_{1, 118} = 3.37$, $P = 0.07$; summer 2013: $F_{1, 118} = 6.17$, $P = 0.01$). Shrub seeds were relatively scarce and did not change consistently with grazing (Table 1). Highly consumed and selected seed species (Pirk & Lopez de Casenave, 2006; Pirk *et al.*, 2009; this study) and preferred seed species (Pirk & Lopez de Casenave, 2011) were much more abundant (79–96%) under light grazing in Llantas (*Aristida* spp., *T. crinita*, *Setaria leucopila*, *B. aristidoides* and *B. barbata*; Table 1).

Ant diet and seed selection

Although seeds were the most abundant item retrieved by *P. mendozanus* under all conditions and seasons, colonies at the heavily grazed sites consumed a higher proportion of flowers and fruits, plant vegetative structures and invertebrates than colonies under the lighter grazing conditions (Fig. 1). Accordingly, diet was usually more diverse under such conditions: in spring 2011, Jagüel $H = 1.3 \pm 0.1$, Llantas $H = 0.37 \pm 0.16$ (Mann–Whitney test, $U = 0$, $P < 0.05$); in spring 2012, Jagüel $H = 1.27 \pm 0.21$, Llantas $H = 0.48 \pm 0.38$ ($U = 3$, $P < 0.05$), in summer 2012, Jagüel $H = 0.74 \pm 0.37$, Llantas $H = 0.5 \pm 0.25$ ($U = 31$, $P = 0.15$), and in summer 2013, Jagüel $H = 0.97 \pm 0.25$, Llantas $H = 0.62 \pm 0.3$ ($U = 7$, $P < 0.05$). On average ($\pm$ SD), seeds represented $85 \pm 5\%$ and $50 \pm 20\%$ of the diet in low and high grazing conditions, respectively (Fig. 1). Grass species prevailed among seeds in the diet, accounting for >85% (Llantas) and >68% (Jagüel) of seeds carried back to the nest (Fig. 2).

Seed selection varied with the grazing regime. *Pogonomyrmex mendozanus* showed a more opportunistic behaviour in the less grazed condition, where the correspondence coefficient between seed-species abundance in diet and soil approached one ($r_c = 0.96$, 95% CI: 0.9–0.98; Fig. 3a). By contrast, ants were highly selective foragers under heavy grazing ($r_c = 0.5$, 95% CI: 0.14–0.74; Fig. 3b). Beyond such differences, there were also some coincidences. The consumption of medium and large seeds of the perennial grasses *Aristida* spp. and *T. crinita* was greater than expected according to their availability in both conditions, whereas several forb and grass seeds (*Chenopodium papulosum*, *H. mendocinum*, *S. leucopila*) were consumed less than expected in Llantas and Jagüel (Fig. 3). Regarding the annual grass seeds, *B. aristidoides* was consumed in proportion to its availability, and *B. barbata* was not positively selected in any case (Fig. 3).

Foraging activity and foraging success

Foraging activity of *P. mendozanus* was more conspicuous in colonies located in the less grazed condition. On average, the number of foragers leaving and returning to the nest each hour was 2.5 times higher in Llantas than in Jagüel (range 1.7–4.3), and this trend was usually consistent between seasons and years (Table 2). Soil surface temperature near the nest entrance was very similar between Llantas and Jagüel (Fig. 4), with spring 2011 being the only exception, when three out of eight hourly records were higher in Jagüel (interaction: $F_{2,13} = 3.97$, $P < 0.001$, grazing level: $F_{1,13} = 30.8$, $P < 0.0001$, Tukey test,

Table 1. Mean soil seed bank density (seeds m^{-2}) of seed species in *Prosopis* open woodlands under light (Llantas) and heavy (Jagüel) grazing pressure in Telteca, central Monte desert, Argentina. Available information on seed consumption by harvester ants is also shown: seeds may be not (x), lowly (lc) or highly consumed (hc); positively (s+),negatively (s−) or not selected (ns); and preferred (p) or not preferred (np).

Seed species	Consumption categories*	Llantas				Jagüel			
		Spring 2011	Summer 2012	Spring 2012	Summer 2013	Spring 2011	Summer 2012	Spring 2012	Summer 2013
Shrubs									
Atriplex lampa	lc s+	0	41	21	21	0	0	0	0
Bulnesia retama	x	0	62	0	0	0	41	0	0
Capparis atamisquea	lc s+	0	0	0	0	0	21	0	0
Lycium spp.	lc ns	21	0	0	0	83	124	21	0
Suaeda divaricata	lc s−	124	0	0	21	21	0	0	0
Total shrubs		**145**	**103**	**21**	**42**	**104**	**186**	**21**	**0**
Perennial grasses									
Aristida spp.	hc s+ p	290	62	62	62	0	21	145	0
Setaria leucopila	lc s− p	166	311	104	104	83	21	41	21
Sporobolus phleoides	lc	62	21	249	0	21	0	83	0
Trichloris crinita	hc s+	518	249	311	41	41	124	104	21
Other		21	103	0	41	0	0		0
Total perennial grasses		**1057**	**746**	**726**	**248**	**145**	**166**	**373**	**42**
Annual grasses									
Bouteloua aristidoides	hc ns	3380	871	788	2840	104	0	0	83
Bouteloua barbata	hc ns	2778	1057	352	62	145	187	41	0
Total annual grasses		**6158**	**1928**	**1140**	**2902**	**249**	**187**	**41**	**83**
Forbs									
Chenopodium spp.	lc s− np	41	21	62	0	104	0	21	21
Heliotropium mendocinum	lc s−	435	332	456	124	41	41	41	21
Euphorbia spp.	lc	0	0	0	41	21	83	0	0
Other		41	21	62	0	104	0	21	21
Total forbs		**517**	**374**	**580**	**165**	**270**	**124**	**83**	**63**
Total seeds		**7877**	**3151**	**2467**	**3357**	**768**	**663**	**518**	**188**

*Lowly/highly consumed seeds (lc/hc) represent less/more than 10% of the diet of at least one out of three harvester ants common in the region (i.e. *Pogonomyrmex mendozanus*, *Pogonomyrmex rastratus* and *Pogonomyrmex inermis*; Pirk & Lopez de Casenave, 2006; Pirk *et al.*, 2009; this study). Positively and negatively selected seeds (s+/s−) were those consumed by *Pogonomyrmex* harvester ants to a greater or lesser extent than expected, according to the seed availability in the field. Not selected seeds (ns) were those consumed in proportion to their availability in the field (Pirk *et al.*, 2009; this study). Seed preferences were evaluated with paired choice experiments and the level of preference of each seed was determined using the normalised David's score corrected for chance (Pirk & Lopez de Casenave, 2011).

$P < 0.05$; Fig. 4). Soil temperature in colonies did not differ between grazing conditions in any other sampling occasion (summer 2012, interaction: $F_{2,13} = 2$, $P = 0.08$, grazing level: $F_{1,13} = 0.09$, $P = 0.77$; spring 2012, interaction: $F_{2,13} = 0.75$, $P = 0.61$, grazing level: $F_{1,13} = 0.14$, $P = 0.71$; summer 2013, interaction: $F_{2,13} = 0.92$, $P = 0.48$, grazing level: $F_{1,13} = 0.31$, $P = 0.58$; Fig. 4).

Pogonomyrmex mendozanus showed an average foraging success of $71 \pm 12\%$ (53–85%) in this study. The number of workers that returned to the nest with solid food was usually higher in Llantas (overall mean: $78 \pm 10\%$) than in Jagüel ($64 \pm 14\%$). Such differences, however, were only significant in spring when foraging success was 15–31% higher in Llantas (Table 3).

Food intake

The mean number of food items entered per colony day^{-1} was 70% (range 58–80%) lower on average in nests located in Jagüel than in Llantas (Fig. 5). Regarding the seeds, the total number was $80 \pm 8\%$ lower at the heavily grazed site

(Fig. 5), and the number of those seeds selected and preferred by *P. mendozanus* was $56 \pm 8\%$ lower at the heavily grazed site. On average, 250 seeds of selected and preferred species entered per colony day^{-1} in Llantas (range 55–553) but only 108 in Jagüel (range 24–242). The number of non-seed items entered per colony day^{-1} did not differ between conditions in spring or showed inconsistent trends in summer (Fig. 5).

Colony density

The density of colonies of *P. mendozanus* was more than six times more abundant on average in the less grazed areas ($U = 0$, $P = <0.01$). Mean ($\pm$ SD) colony density was 33.3 ± 14.0 ha^{-1} (range 20–52) in Llantas, and 5.3 ± 6.2 ha^{-1} in Jagüel (range 0–16).

Discussion

Grazing by domestic animals triggered both behavioural and numerical responses of *P. mendozanus*, and the reduction of
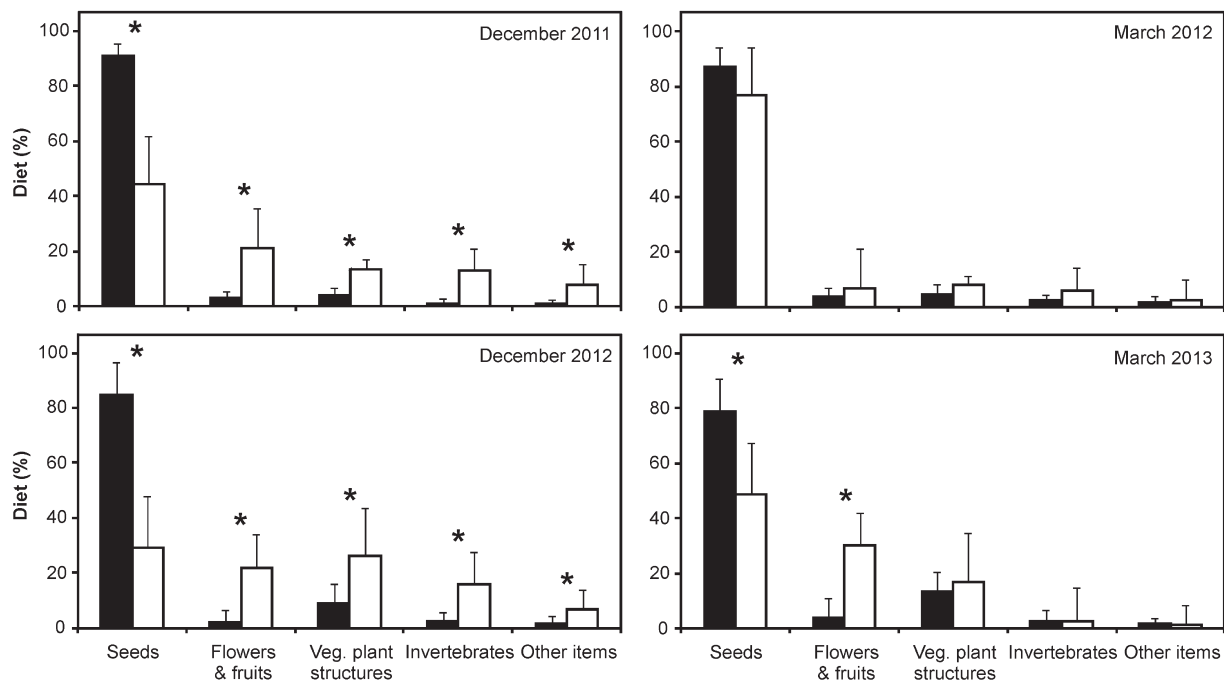
Fig. 1. Mean (+ SD) percentage of seeds, fruits and flowers, vegetative plant structures, invertebrates and other items in the diet of *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (black bars; Llantas) and heavy (white bars; Jagüel) grazing pressure in Telteca, central Monte desert of Argentina. Asterisks indicate significant differences between grazing regimes (*t*-test or Mann–Whitney test, *P* < 0.05).

preferred seeds in the soil could have been the link between the presumed cause and its effects. The abundance of grass seeds fell notably, and the most affected species (a reduction of 78–96%) were those highly consumed, selected and/or preferred by the ants (Pol *et al.*, 2014). Less attractive seeds, such as most forb seeds, also suffered reductions but they were less consistent, as clear differences between conditions were detected in only two of the four samplings. Our results coincided with those reported for other deserts (O'Connor & Pickett, 1992; Sternberg *et al.*, 2003; Dreber & Esler, 2011) and, particularly, for the Monte desert (Blendinger & Ojeda, 2001; Gonnet, 2001; Milesi *et al.*, 2002; Pol *et al.*, 2014), confirming a generalised negative effect of livestock grazing on the main food resources of seed-eating animals.

Pogonomyrmex mendozanus had a more diverse diet under heavy grazing, with a lower proportion of seeds and a higher proportion of invertebrates, flowers, fruits and vegetative plant structures. Harvester ants usually show flexible foraging conduct (Davidson, 1977; Gordon, 1991; Melhop & Scott, 1983; Pirk *et al.*, 2009; Belchior *et al.*, 2012), behaving as generalists or expanding specialists (i.e. a forager that specialises on one food type until it falls below some threshold value, at which point the forager begins to include less preferred food types in their diet; Heller, 1980). Among seeds, however, grasses always prevailed in the diet in both grazing conditions where foragers carried almost the same grass species. In spite of the wider general diet under heavy grazing, *P. mendozanus* was a more selective granivore there. Many seed species were positively or negatively selected, and the correspondence coefficient between seed-species abundance in soil and diet was lower

than under light grazing (i.e. 0.5 vs. 0.96). High selectivity of some seed items under low seed availability is one type of context-dependent foraging behaviour, which has been detected in other seed-eating organisms of the Monte desert (i.e. birds; Marone *et al.*, 2015).

In mature colonies, the rates of foraging activity and foraging success may decline when seed resources are scarce in the habitat (Gordon *et al.*, 2008; Pol *et al.*, 2011, 2015). Gordon *et al.* (2008) proposed that a reduction in seed abundance would lead to decreased foraging activity via a reduction in foraging success, but our results did not support the idea as foraging success was not consistently lower under heavy grazing. A related explanation is that seed quality modulates foraging activity. There is some evidence of seed quality detection in *Pogonomyrmex* ants: Greene *et al.* (2013) proposed that workers of *Pogonomyrmex barbatus* (F. Smith) distinguish between foragers that return to the nest with seeds from those that return without seeds by detecting odours of seeds (e.g. from oleic acid). If a similar mechanism operated in *P. mendozanus*, its workers might eventually detect grass seeds entering the nest and increase foraging activity as a response to high-quality food. The rates of foraging activity and foraging success may also decline in grazed areas if soil temperature rises owing to an increase of the proportion of exposed soil. Such an explanation was inappropriate for Telteca, however, as the soil temperature regime was very similar under both grazing conditions.

Expanded diet and reduced foraging activity and foraging success of *P. mendozanus* under heavy grazing had negative consequences on colony food intake, especially in the number of grass seeds harvested. Under certain circumstances, a harsh
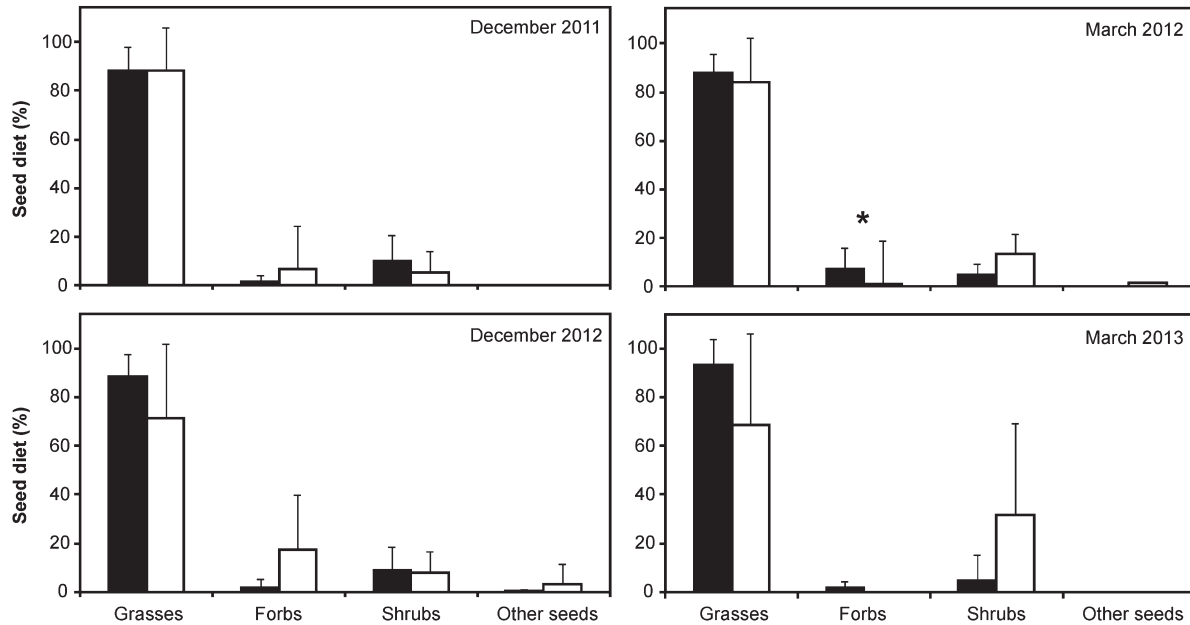
Fig. 2. Mean (+ SD) percentage of seeds of different plant groups (grasses, forbs, shrubs and other seeds) in the diet of *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (black bars; Llantas) and heavy (white bars; Jagüel) grazing pressure in Telteca, central Monte desert of Argentina. Asterisks indicate significant differences between grazing regimes (*t*-test or Mann–Whitney test, $P < 0.05$).
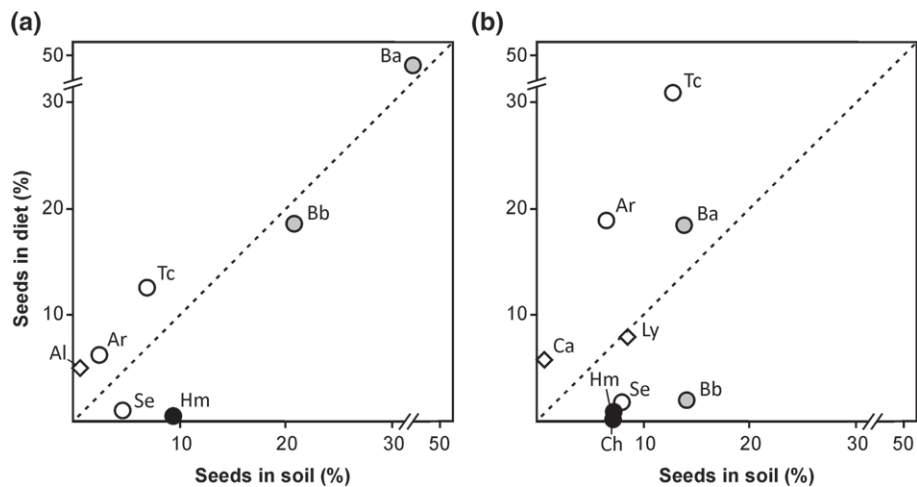

Fig. 3. Relationship between the relative abundance, expressed as percentages, of the most abundant seeds (>5%) in the soil bank and/or in the diet of *Pogonomyrmex mendozanus* ants in *Prosopis* open woodlands under light (a; Llantas) and heavy (b; Jagüel) grazing pressure conditions in Telteca, central Monte desert of Argentina. Black dots correspond to species of forbs, open dots to perennial grasses, grey dots to annual grasses and open diamonds to species of shrubs. The broken line represents the plane of equivalence of the occurrence in soil and in diet for each seed species. Ar, *Aristida* spp.; Tc, *Trichloris crinita*; Se, *Setaria leucopila*; Ba, *Bouteloua aristidoides*; Bb, *Bouteloua barbata*; Ch, *Chenopodium papulosum*; Hm, *Heliotropium mendocinum*; Al, *Atriplex lampa*; Ca, *Capparis atamisquea*; Ly, *Lycium* spp.

reduction in the amount of grass seeds may lead to ant nutritional imbalance and starvation, as grass seeds are a rich source of carbohydrates (Ríos *et al.*, 2012), which play an important role in ant growth and reproduction (Bono & Herbers, 2003; Feldhaar, 2014). In particular, workers require carbohydrates as the main energy source, and their deprivation increases worker mortality (Kay *et al.*, 2006; Bazazi *et al.*, 2016). Nutrient

imbalance may also prevent the production of sexual offspring, especially the more costly queens (Smith, 2007). It also reduces the fat body content and body size of workers and queens (Smith, 2007; Smith & Suarez, 2010), worsening the reproductive potential of colonies (Wiernasz & Cole, 2003). Although these potential effects of nutrient shortage and starvation should be further explored in this system, we partially corroborated some

Table 2. Foraging activity rate (mean ± SD) of *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (Llantas) and heavy (Jagüel) grazing pressure in Telteca, central Monte desert of Argentina.

Sampling occasion	Llantas	Jagüel	U	P
December 2011	2964 ± 527 (6)	1440 ± 303 (6)	0	0.002
March 2012	1898 ± 760 (6)	436 ± 430 (6)	2	0.01
December 2012	750 ± 309 (6)	442 ± 377 (6)	10	0.2
March 2013	656 ± 297 (6)	241 ± 98 (6)	2	0.01
Overall mean	1567 ± 1089	640 ± 542	–	–

Foraging activity was measured as the number of workers leaving and returning to the nest day^{-1}. Results from the Mann–Whitney test and the number of colonies sampled (*n*) are shown.
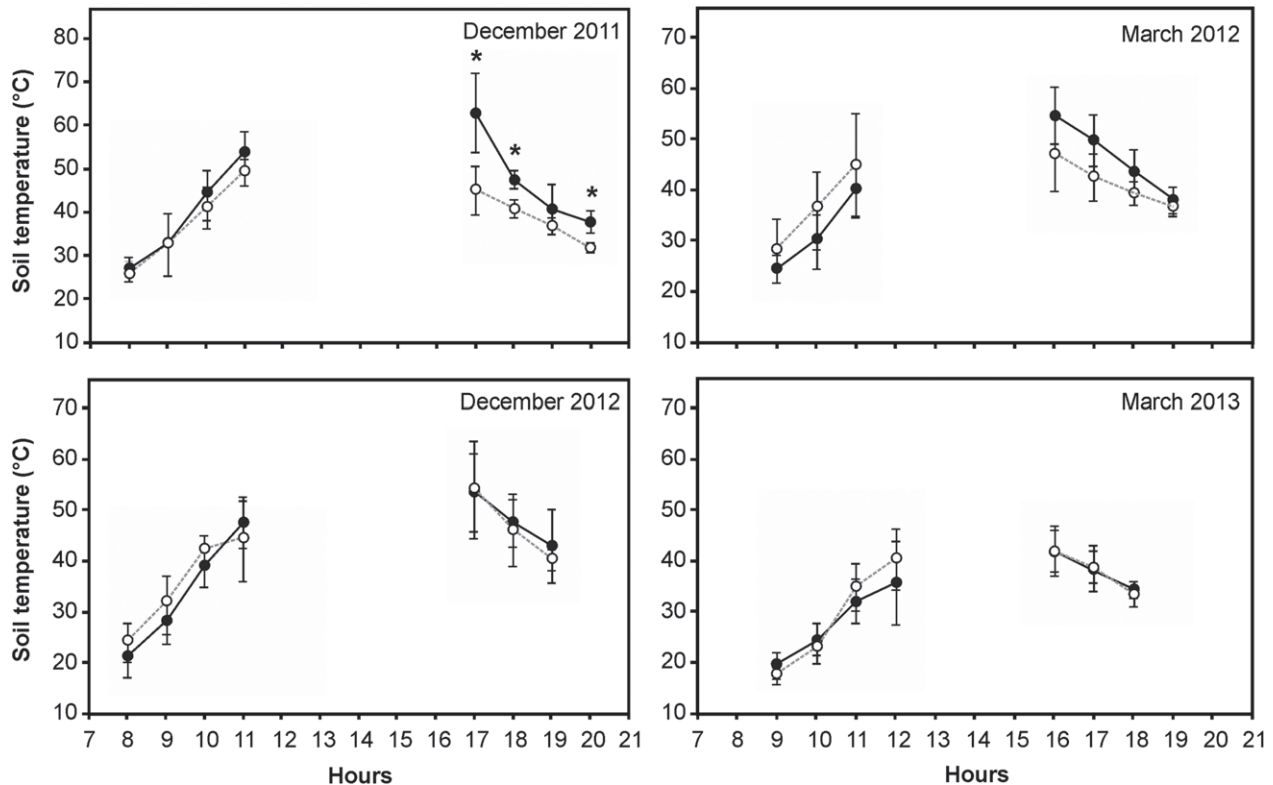
Fig. 4. Mean (± SD) soil surface temperature next to the nest entrances of *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (black dots; Llantas) and heavy (white dots; Jagüel) grazing pressure in Telteca, central Monte desert, Argentina. Asterisks indicate significant differences between grazing levels (two-way ANOVA, $P < 0.05$; Tukey test, $P < 0.05$).

Table 3. Foraging success (mean ± SD) of *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (Llantas) and heavy (Jagüel) grazing pressure in Telteca, central Monte desert of Argentina.

Sampling occasion	Llantas	Jagüel	t	P
December 2011	77 ± 14 (10)	62 ± 18 (10)	−2.16	0.04
March 2012	85 ± 7 (11)	84 ± 11 (10)	−0.34	0.74
December 2012	84 ± 10 (7)	53 ± 28 (9)	−2.84	0.01
March 2013	64 ± 38 (7)	57 ± 42 (7)	−0.31	0.76
Overall mean	78 ± 10	64 ± 14	–	–

Foraging success is expressed as the proportion (%) of foragers returning with food to the nest. Results from the *t*-test and the number of colonies sampled (*n*) are shown.
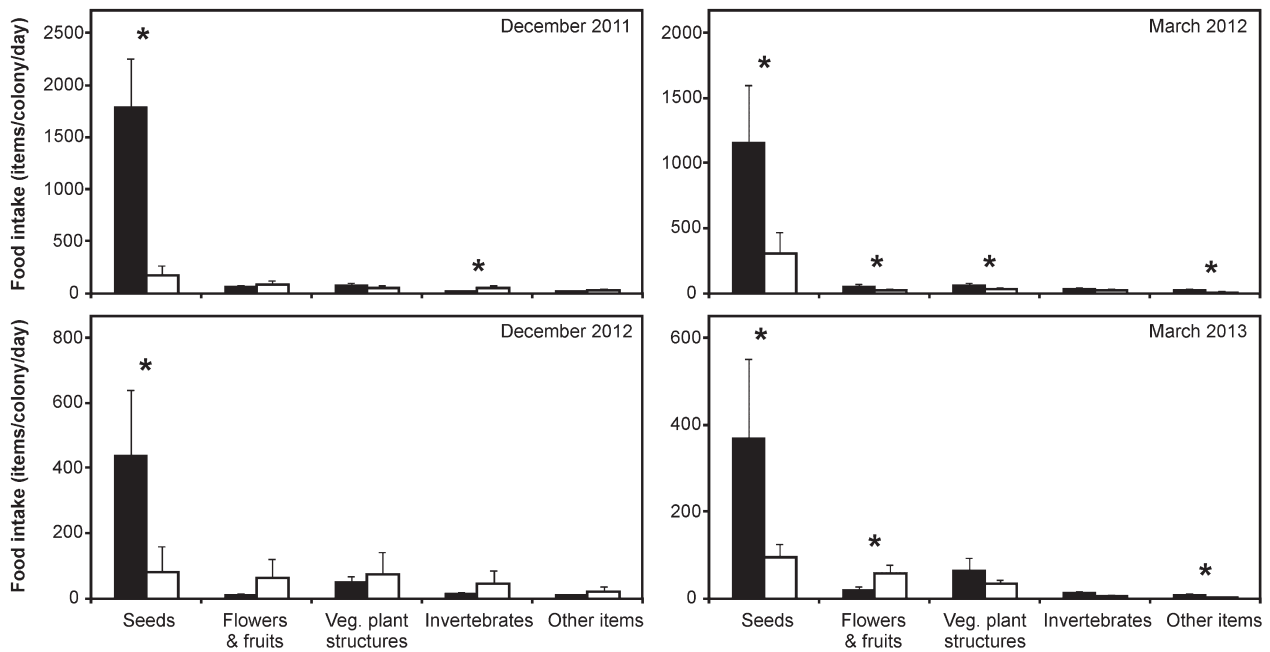
Fig. 5. Mean (+ SD) of seeds, flowers and fruits, vegetative plant structures, invertebrates and other items that are entered during a day into *Pogonomyrmex mendozanus* colonies in *Prosopis* open woodlands under light (black bars; Llantas) and heavy (white bars; Jagüel) grazing pressure in Telteca, central Monte desert of Argentina. Asterisks indicate significant differences between grazing regimes (*t*-test or Mann–Whitney test, $P < 0.05$).

consequences of the causal chain: ant colony density decreased about 84%, associated with a harsh seed decline in the heavily grazed areas. The same pattern has been reported in other studies that explicitly considered changes in resource availability (Crist & Wiens, 1996; Sorvari & Hakkarainen, 2005, 2007).

Grass seed reduction triggered behavioural responses in *P. mendozanus*, which expanded its diet and reduced its foraging activity remarkably. Behavioural flexibility might be an important adaptation that copes with habitat deterioration, increasing the resilience and viability of ant populations. However, behavioural responses of *P. mendozanus* had complex and even opposite effects on ant performance: their net effect was a deterioration of colony food intake and, probably, of the nutritional condition of ants. Behavioural flexibility may therefore be insufficient to prevent population declines of these ants in scenarios of global change, such as those related to heavy grazing in the Monte desert.

Acknowledgements

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