Occurrence of Ctenomys mendocinus in a High-Altitude Cold Desert: Effect on Density, Biomass, and Fitness of Sagebrush Plants

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Occurrence of *Ctenomys mendocinus* in a high-altitude cold desert: effect on density, biomass, and fitness of sagebrush plants

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ABSTRACT

In arid and semiarid ecosystems, subterranean herbivorous rodents play an important role in determining the composition, function, and structure of plant communities. We hypothesized that in a high-altitude cold desert in the southern Puna region of Argentina, *Ctenomys mendocinus* (mendocino tuco-tuco), a subterranean herbivorous rodent, may increase dominance of the shrub *Artemisia mendozana* (sagebrush). We performed an observational study to assess factors affecting the abundance and fitness of *A. mendozana* in southern Puna, on sites co-inhabited and undisturbed by *C. mendocinus*. Density, biomass, plant height, number of fruits per plant, number of seeds, and seed size of *A. mendozana* were higher in mendocino tuco-tuco–disturbed areas.

Because the abundance and reproductive ability of sagebrush increase in areas inhabited by mendocino tuco-tucos, *C. mendocinus* may function as an ecosystem engineer in southern Puna. We suggest further manipulative experimental studies be conducted to clarify the role of this subterranean rodent in this ecosystem.

INTRODUCTION

Many subterranean and burrowing mammals have been identified as keystone species (a species with strong effects on community structure or ecosystem function, relative to its abundance; Power et al., 1996) and/or ecosystem engineers (i.e., organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials; Jones et al., 1994). The important impacts of subterranean and burrowing mammals on ecosystems manifest through activities such as feeding on particular vegetation and modifying soil biogeochemistry (Kotliar, 2000; Reichman and Seabloom, 2002; Zhang et al., 2003; Berke, 2010; Hagenah and Bennett, 2013). These processes can modify the physical environment through critical interactions that generate effects at multiple ecological levels (patch, population, community, ecosystem, and landscape; Eldridge and James, 2009; Hagenah and Bennett, 2013; Wright and Jones, 2006).

In arid and semiarid ecosystems, subterranean herbivorous rodents may affect the structure of plant communities in at least two ways: directly, by consuming whole plants or parts of them (Campos et al., 2001; Lara et al., 2007; Reichman, 2007; Van Nimwegen et al., 2008); and indirectly, by their digging activities, moving soil and altering its physical and chemical features (Reichman and Seabloom, 2002). A recent review of disturbances by small mammals reported effects on plant species richness, diversity, and biomass, but almost all studies reviewed were conducted at a community level (Root-Bernstein and Ebensperger, 2012) without regard for effects at the population level.

The mendocino tuco-tuco, *Ctenomys mendocinus* (Rodentia, Ctenomyidae) is a medium-sized subterranean herbivorous rodent (145–180 g; 247–262 mm) restricted to the arid lands of central west Argentina

(Rosi et al., 2005). *C. mendocinus* builds complex burrow systems with several entrances (usually closed), some of them with soil mounds near the entrances and others called feeding holes, which are immediately beside the plants they consume (Reig et al., 1990; Rosi et al., 1996). Previous research on the ecology of *C. mendocinus* describes it as a potential ecosystem engineer because of its burrowing and feeding activities, which decease the spatial heterogeneity of soil nutrients (Borruel et al., 1998; Campos et al., 2001; Lara et al., 2007; Tort et al., 2007; Albanese et al., 2010).

Generally speaking, herbivory on dominant plant species has been shown to increase the possibility of establishment of new plants due to competition reduction (Campos et al., 2001; Lara et al., 2007; Albanese et al., 2010). Herbivory may also alter plant morphology because of selective feeding on specific plant tissues, as well as plant reproduction (Camin and Madoery, 1994; Rosi et al., 2003). Burrowing activities may increase fitness of plants by increasing nutrient concentrations (N, P, K) required for flowering and fruit set (Malizia et al., 2000; Lara et al., 2007).

Although *Ctenomys* sp. has been suggested to be an ecosystem engineer, its role in particular ecosystems has not yet been formally assessed. Previous research in the southern Puna desert showed that the mendocino tuco-tuco may increase dominance of the shrub *Artemisia mendozana* (sagebrush) in plant communities (80% of total plant cover; Lara et al., 2007). The mendocino tuco-tuco feeds on almost all plant species in the southern Puna desert, including *A. mendozana* (2.85%; Rosi et al., 2003). Despite this pattern, however, the highest sagebrush cover occurs at sites inhabited by this rodent (Lara et al., 2007). In the present study, we assess the factors that may contribute to the abundance of *A. mendozana* in southern Puna, at paired sites inhabited and relatively undisturbed by *C. mendocinus*. We hypothesized that the mendocino tuco-tuco generates a favorable environment for sagebrush plants, increasing their cover and reproductive ability. Specifically, we predicted: (1) sagebrush density and biomass will be higher at sites inhabited by mendocino tuco-tucos, (2) individual sagebrush plants will be larger (in weight and height) at sites inhabited by mendocino tuco-tucos, (3) the number of flowers and fruits per plant, and/or the number of seeds per fruit will be higher at sites inhabited by mendocino tuco-tucos, and (4) total seed production will be greater at sites inhabited by mendocino tuco-tucos.

METHODS

Study Site

This study was conducted in Don Carmelo Multiple Use Private Reserve, a protected area of about 40,000 ha, located in La Invernada valley (31°10′S, 69°46′W, at 3000 m a.s.l.), San Juan Province, Argentina, which lies within the Puna desert (Martínez Carretero, 1995; Reboratti, 2006). The vegetation is composed of low xerophytic shrubs and grasses, with large areas of bare soil (Márquez, 1999; Lara et al., 2007). Climate in the Puna is characterized by long, dry cold periods and a wide daily temperature range; rainfall occurs primarily in summer and does not exceed 100 mm a year (Martínez Carretero, 1995; Reboratti, 2006). In Don Carmelo, there are temperature records only for 2010. For this year, mean annual temperature was 8.15 °C, maximum absolute temperature was 26.00 °C, and minimum absolute temperature was −22.00 °C. Snowfall occurs mainly between May and October, and winter snow can reach 50 cm depth although it usually remains on the ground for less than 15 days (personal observation).

Sampling Design

To assess the impact of tuco-tucos on *A. mendozana*, we carried out a comparative factorial study both at the beginning of the flowering period of sagebrush and in its fruiting period (wet and dry seasons, respectively). We randomly selected four sites within the community and chose two types of areas in each site: (1) areas with high density of holes (3.46/2 m²) and mounds (1.82/2 m²) of mendocino tuco-tucos (areas highly disturbed by tuco-tucos = "disturbed"), and (2) areas with low density of holes (0.36/2 m²) and mounds (0.25/2 m²) of mendocino tuco-tucos (areas relatively undisturbed = "undisturbed"; Lara et al., 2007). In each area (disturbed and undisturbed), we established three 8-m-long parallel transects (replicates) with 4 sampling quadrats (1 × 1 m) at 1-m intervals. In each quadrat we recorded number and height of sagebrush individuals. During the flowering and fruiting periods we collected the individuals in each quadrat in order to record other parameters in the laboratory. Clipped plants were oven-dried at 70 °C for 24 h, weighed, and biomass was converted to kg per 12 m². The number of flowers present on each plant was recorded. During the fruiting period and before seed dispersal, we quantified the number of fruits per sagebrush plant and estimated seed number per plant by multiplying the total number of fruits by the average number of seeds in 10 fruits of each plant. Seed size was estimated by measuring the area and perimeter of seeds from 20 samples of 20 seeds per site (10 from disturbed sites and 10 from undisturbed sites) using a scanner according to the method of image analysis proposed by O'Neal et al. (2002) and the Scion Image for Windows software version 4.0.3.2 (Scion Corporation, 2000–2001).

Finally, we estimated seed set, total seed production per plant, and total seed production per square meter. To estimate seed set, we divided the mean number of seeds produced per plant by the mean number of flowers per plant. To estimate total seed production per square meter, we multiplied the mean number of plants per square meter by the mean number of fruits per plant and by the mean number of seeds per fruit.

Statistical Analysis

To evaluate the effect of *C. mendocinus* perturbation on population (density, biomass), individual (height, weight) and reproductive (flowers, fruits, seeds) responses of *A. mendozana*, we obtained, for each variable, an average value in each replicate. We used Linear Mixed Models (LMMs) with Gaussian error distributions as implemented by nlme package (Bolker et al., 2008; Zuur et al., 2009; Pinheiro et al., 2016) within the R computational environment version R 3.2.5 (R Development Core Team, 2016). Disturbance was included as a fixed factor with two levels: disturbed and undisturbed. Site and season were defined as random factors in LMMs. In order to evaluate the effect of tuco-tucos on reproductive variables, we included plant size (weight and height) in LMMs as a covariate. To assess seed size (perimeter and area) in disturbed and undisturbed areas we also used LMMs with site as a random effect. We determined the significance of the fixed effects using likelihood ratio tests (Bolker et al., 2008). Results are presented as mean ± standard error (SE), and for null hypothesis testing, statistical tests were considered significant at $\alpha < 0.05$.

RESULTS

Population Level

LMM analyses revealed that density of sagebrush plants was significantly higher in highly disturbed areas (22.41 ± 1.63 vs. 14.45 ± 1.09 plants m^{-2}; $p < 0.0001$; Table 1 and Fig. 1, part A). This pattern was also evident for plant biomass (disturbed = 684.11 ± 79.36 kg 12 m^{-2} and undisturbed = 495.25 ± 66.63 kg 12 m^{-2}, respectively; $p = 0.0002$; Table 1 and Fig. 1, part A).

Individual Level

Sagebrush plant size was measured through the proxy variables weight and height of plants. Disturbance by mendocino tuco-tucos affected the height but not the weight of individual sagebrush plants (Table 1 and Fig. 1, part B), with plants being slightly taller in disturbed areas (17.22 ± 0.62 cm vs. 15.33 ± 0.64 cm; $p = 0.001$; Fig. 1, part B).

Reproduction Level

During the flowering period we collected a total of 440 individuals from disturbed and undisturbed areas. The number of flowers per sagebrush plant did not vary with *C. mendocinus* disturbance (32.79 ± 3.53 and 30.90 ± 4.58; $p = 0.60$; Table 1 and Fig. 1, part C). In the fruiting period we collected 458 individuals from both areas. Sagebrush plants in disturbed areas produced more than twice the number of fruits compared to those in undisturbed areas (12.19 ± 1.40 vs. 4.86 ± 0.92 fruits m^{-2}; $p = 0.004$; Fig. 1, part C). Furthermore, the number of seeds per sagebrush plant was higher in disturbed than in undisturbed areas (26.36 ± 1.27 and 12.17 ± 1.93, respectively; $p = 0.0006$; Table 1 and Fig. 1, part D). In relation to seed size, we observed slightly larger seeds in disturbed areas, there being a near-significant result for area and a significant effect for perimeter ($p = 0.06$ and $p = 0.04$, respectively; Table 1 and Fig. 1, part D).

We found no differences in number of flowers per plant between disturbed and undisturbed areas, but seed set was significantly higher in disturbed areas (12.5 ± 1.58 vs. 26.6 ± 1.2; $p = <0.001$; Table 2). In addition, seed production per square meter was nearly eight times greater in disturbed than in undisturbed areas (Table 2).

DISCUSSION

Measures of individual and population health, and reproductive success, of *A. mendozana* increased significantly in disturbed areas, suggesting that activities of the mendocino tuco-tuco affect sagebrush plants positively.

We found that sagebrush density increased in disturbed areas. This finding is consistent with Lara et al. (2007), who found a significant increase in number of *A. mendozana* shrubs in mendocino tuco-tuco–disturbed areas. Sagebrush represented 47% of the total individual plants recorded in undisturbed areas, whereas in disturbed areas, its dominance increased as much as 80% (Lara et al., 2007). Previous research on the diet and herbivory of *C. mendocinus* shows that it mainly consumes herbs (such as *Stipa* sp. and *Elymus erianthus;* Rosi et al., 2003) and other shrubs (*Lycium chanar, Junellia uniflora*, and *Senecio* spp.; Tort et al., 2004), but avoids sagebrush plants, probably because of their higher concentrations of plant secondary metabolites (Golob et al., 1999). Mendocino tuco-tucos may feed on and kill competing shrubs instead of sagebrush (the number of dead non-sage shrubs in disturbed areas is higher than in undisturbed ones: 3.57 and 1.43, respectively; Lara et al., 2007; N. Andino

TABLE 1

Effect of the mendocino tuco-tuco on population, individual, and reproduction levels of *A. mendozana*. Reported values represent results of Linear Mixed Models for explanatory variables describing variation in population (Density, Biomass), individual (Weight, Height) and reproductive (Flowers, Fruits, and Seeds) parameters and seed size in sagebrush plants, considering disturbance situation (DS) caused by mendocino tuco-tucos as fixed factor. We used Site and Season as random factors. Effects of fixed factor is analyzed using the likelihood ratio test (LRT).

Response variable	Fixed factor	Estimate	Standard Error	P value (LRT)
Population parameters				
	Intercept	−7.45	1.48	
Density	DS	22.41	1.96	<0.0001
	Intercept	−188.25	92.47	
Biomass	DS	683.09	96.17	0.04
Individual parameters				
	Intercept	−0.06	1.01	
Weight	DS	10.81	1.79	0.94
	Intercept	−1.88	0.56	
Height	DS	17.22	2.28	0.001
Reproductive parameters				
	Intercept	2.47	4.72	
	DS	−23.14	20.14	0.54
	Plant Height	2.63	2.07	
Flowers	Plant Weight	0.30	0.4	
	Intercept	6.84	2.07	
	DS	11.62	6.89	0.001
	Plant Height	−0.21	0.39	
Fruits	Plant Weight	−0.38	0.55	
	Intercept	−7.71	9.38	
	DS	12.01	2.83	<0.0001
	Plant Height	1.44	0.75	
Seeds	Plant Weight	0.008	0.53	
Seed size				
	Intercept	4.19	0.12	
Perimeter	DS	0.25	0.13	0.05
	Intercept	1.06	0.07	
Area	DS	0.11	0.06	0.08

and C. E. Borghi, personal observations), which would promote increased density of sagebrush. *C. talarum* also reduces the competition stimulating plant biomass and changing plant species composition directly adjacent to the disturbances in a coastal grassland (Malizia et al., 2000). Galiano et al. (2014) suggested a positive effect of *C. minutus* on the abundance of grasses by relaxing competition in an area in a south Brazilian coastal plain. Furthermore, in our study site, Lara et al. (2007) found that the activity of mendocino tuco-tucos increased N (1000 ppm), K (410 ppm), and P (7.90 ppm) concentrations in bare soil in relation to undisturbed areas (N =
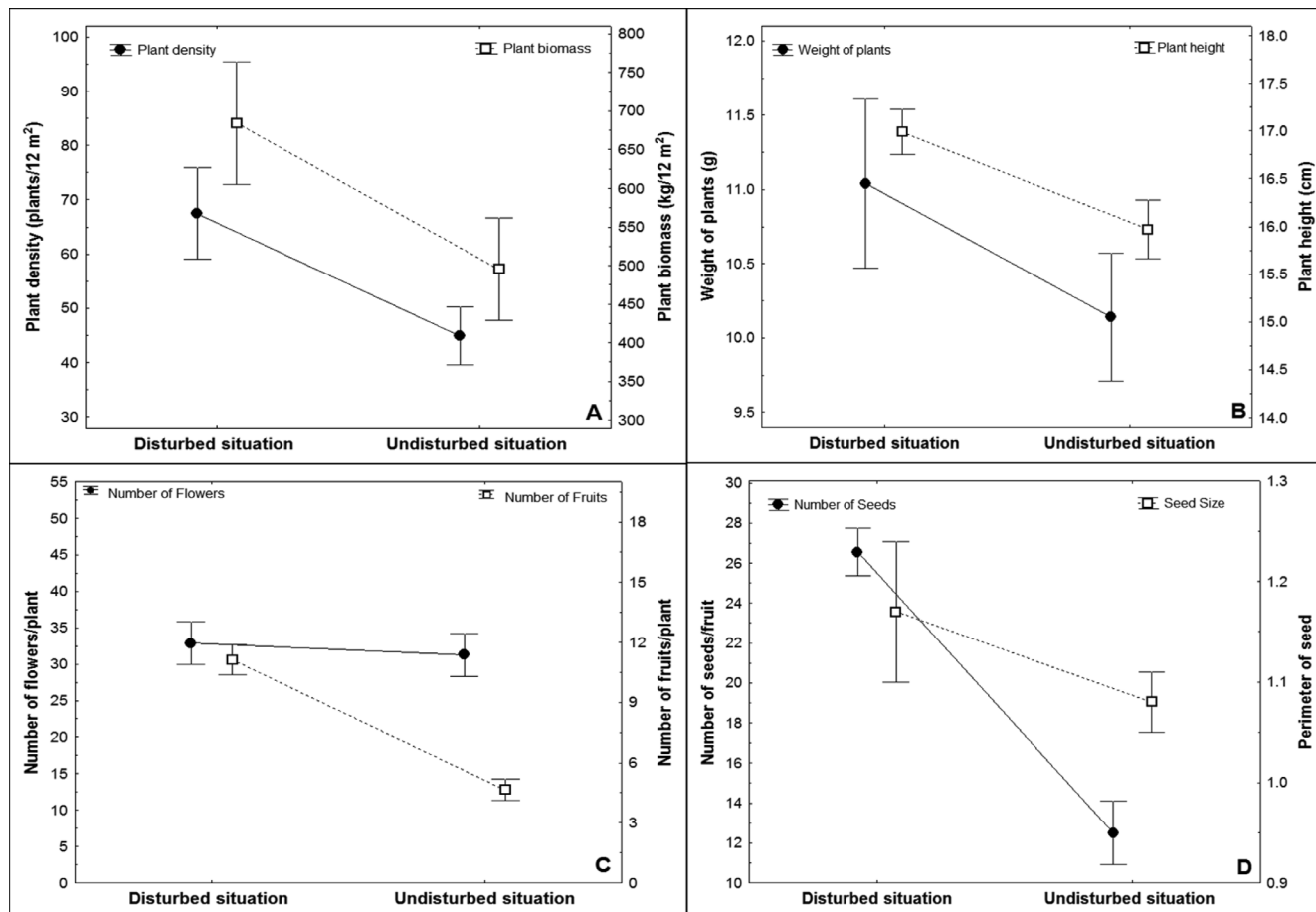
FIGURE 1. Effect of the mendocino tuco-tuco on population, individual and reproductive parameters of sagebrush. Values shown are mean (±SE) of plant density and biomass (A), plant weight and height (B); number of flowers and fruits per plant (C) and seed size (D) in disturbed and undisturbed areas by mendocino tuco-tucos.

TABLE 2

Population, individual, and reproductive parameters of sagebrush in disturbed and undisturbed areas by mendocino tuco-tucos.

Mean number	Undisturbed area mean (SE)	Disturbed area mean (SE)	*p* value
Plants m^{-2}	44.88(5.37)	67.50(8.38)	0.005
Flowers plant^{-1}	31.30 (2.78)	32.90 (2.94)	0.25
Fruits plant^{-1}	4.65(0.55)	11.12(0.75)	<0.001
Seed set	12.51(1.58)	26.56(1.2)	<0.001
(Seeds fruit^{-1})			
Seeds plant^{-1}	58.17	295.35	
Seeds m^{-2}	2610.74	19,935.94	

Note: To estimate the mean number of seed per m², we multiplied: (mean number of plants per m²) ★ (mean number of fruits per plant) ★ (mean number of seeds per fruit).

800 ppm, K = 340 ppm, P = 7.6 ppm), potentially facilitating sagebrush establishment and density in disturbed areas. In a coastal grassland, *C. talarum* positively affected *Poa lanuginosa* biomass by increasing mineralization rates (Malizia et al., 2000). Similar positive effects of fossorial rodents on plants have been found in the Spanish Pyr-

enees for *Microtus duodecimcostatus,* which indirectly favors the abundance of *Cirsium acaule*, *Sanguisorba minor*, *Meum athamanticum* (Gómez-García et al., 1995), and *Merendera montana* (Gómez-García et al., 2004). Also, *Cryptomys hottentottus hottentottus* positively influenced *Lolium multiflorum, Avena barbata*, and *Lessertia rigida* by

increasing soil nutrients (Hagenah and Bennett, 2013). Moreover, in a semiarid grassland in northern China, *Artemisia* spp. benefited from deposition of herbivore excreta on the soil, which increased nutrient concentration in patches. As a result, *Artemisia* spp. became the dominant species in this degraded grassland with heavy grazing (Wang et al., 2002).

The reproduction of sagebrush was also correlated with disturbance by mendocino tuco-tucos. Specifically, flower production was similar in undisturbed and disturbed areas but the number of fruits and seeds increased in the latter areas. The positive influence on reproduction of sagebrush plants can be explained by direct and indirect activities of this subterranean herbivorous rodent. Some studies have found that the impact of herbivory on reproduction depends on which part of the plant is affected. For example, removal of the leaf does not affect reproduction, whereas removal of flowering structures does affect reproduction (Maschinski and Whitham, 1989; Paige, 1992; Louda and Potvin, 1995; Spotswood et al., 2002). The mendocino tuco-tuco, like *C. australis* and *C. talarum*, consumes the aerial vegetative fraction of plants rather than their reproductive fraction (Comparatore et al., 1995). Albanese et al. (2010) reported that leaves are the most representative item among plant parts (89.51%) in the mendocino tuco-tuco's diet in the lowland Monte desert. In our study population, the mendocino tuco-tuco consumes sagebrush when almost no other plants are available (Rosi et al., 2003; Lara et al., 2007), and when herbivory occurs on sagebrush, the tuco-tuco feeds on only the vegetative fraction (Comparatore et al., 1995). Additionally, defoliation may have differential effects on plant reproduction depending on when it occurs. Studies of the shrub *Piper arieanum* found that, when leaves were removed several months before flowering time, the plant suffered a large loss in reproductive output, but when the same treatment was administered just before flowering, there was no response (Marquis, 1984, 1992). Mendocino tuco-tucos mainly consume leaves of sagebrush plants during autumn (0.82%) and winter (4.40%; Rosi et al., 2003). Our study was performed during autumn just before sagebrush flowering, at a time when herbivory would likely have only minor effects on reproduction (Marquis, 1984; Maschinski and Whitham, 1989; Marquis, 1992; Spotswood et al., 2002).

The activities of mendocino tuco-tucos may also have indirect positive effects on sagebrush reproduction. Burrowing activities by mendocino tuco-tucos may affect soil structure and nutrient availability in the studied community (Lara et al., 2007). Nutrients, in particular N and P, are important to plant reproduction because they are required for flowering and fruit set. In our study area, mendocino tuco-tucos increase nutrient concentration in disturbed compared to undisturbed areas, generating a favorable environment for sagebrush plants, and potentially increasing reproductive output per square meter in disturbed areas. In disturbed areas, sagebrush produce more seeds and slightly larger seeds than in undisturbed areas. This could be a consequence of genetic differences in populations of *A. mendozana*. Genetic and/or environmental factors (including *C. mendocinus* disturbance) may lead to expression of different reproductive strategies at disturbed and undisturbed sites (Rapoport, 1982).

In conclusion, the results of both Lara et al. (2007) and the current study show an increase in the abundance of sagebrush and an improvement of its reproductive ability in areas affected by mendocino tuco-tucos in southern Puna. These results suggest that *C. mendocinus* acts as an ecosystem engineer in the Puna Desert. Even though our study design does not allow us to demonstrate unequivocally that the increase in the reproductive ability of sagebrush is caused by mendocino tuco-tucos, it enables us to propose a potentially important relationship between tuco-tucos and the population of *Artemisia mendozana*. The relationship involved seems to entail an effect on nutrient availability, plant cover, and reproductive success in sagebrush plants. We suggest further manipulative experimental studies to allow insight into the causal role of this subterranean rodent in this ecosystem.

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