Ecología Austral 16:1-6. Junio 2006
Asociación Argentina de Ecología

Bark consumption of creosote bush (*Larrea cuneifolia*) by cuises (*Microcavia australis*): effect on branch survival and reproduction

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ABSTRACT. Locally, mammalian herbivores may have significant effects on the abundance and fitness of plant species. This study focuses on the interaction between cuises (*Microcavia australis* –Rodentia-) and creosote bush (*Larrea cuneifolia* –Zygophyllacea-), which is a widespread and ecologically dominant evergreen shrub in the Monte Desert of Argentina. Specifically, we examined the probability of plants being gnawed by cuises in relation to branch diameter and distance to cuis colonies. Additionally, we assessed the effect of gnawing by cuises on branch condition, production of flowers and fruits and branch survival. In general, gnawing by cuises negatively affects creosote bush plants. The likelihood of being gnawed is higher for branches of smaller diameter and in plants growing closer to cuis colonies. Also, cuises significantly affect the condition, production of reproductive structures and survival of creosote bush branches. This, in turn, may have a long-term effect on the spatial distribution of creosote bush plants in this ecosystem.

[Keywords: Argentina, debarking, Monte desert, plant-animal interaction, plant condition, reproductive structures, rodent]

RESUMEN. Consumo de corteza de jarilla (*Larrea cuneifolia*) por cuises (*Microcavia australis*): efecto sobre la supervivencia de ramas y la reproducción: A nivel regional, la herbivoría producida por mamíferos puede tener efectos significativos sobre la abundancia y el éxito reproductivo de las plantas. El presente trabajo estudia la interacción entre los cuises (*Microcavia australis* –Rodentia-) y la jarilla (*Larrea cuneifolia* –Zygophyllacea-). Este arbusto es la especie vegetal ecológicamente dominante en el Monte árido de Argentina. Se examinó la probabilidad de las plantas de ser roídas por los cuises en relación con el diámetro de las ramas y la distancia a las colonias y el efecto de las roídas sobre las plantas (condición y supervivencia de las ramas, producción de pimpollos, flores y frutos). En general, los resultados mostraron que las roídas en la corteza afectaron negativamente a las jarillas. El daño por roídas fue mayor en las ramas de menor diámetro y en las plantas más cercanas a las colonias de cuises. La herbivoría por cuises afectó la condición y producción de estructuras reproductivas así como también la supervivencia de las ramas de jarilla. De esta manera, la herbivoría por cuises podría, a largo plazo, afectar la distribución espacial de las jarillas en este ecosistema.

[Palabras clave: Argentina, descortezado, Monte árido, interacciones planta-animal, condiciones de plantas, estructuras reproductivas, roedores]

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Recibido: 10 de mayo de 2005; Fin de arbitraje: 23 de agosto de 2005; Revisión recibida: 16 de noviembre de 2005; Aceptado: 11 de febrero de 2006

INTRODUCTION

Herbivores can directly affect plant species by consuming leaves, twigs and other parts, or indirectly by affecting plant competition, altering nutrient cycles and disturbing soils (Ritchie & Olff 1999). Herbivores can also exert a strong selective influence on plants by increasing mortality and by removing biomass that might otherwise be allocated to growth or reproduction (Coley et al. 1985). Through these direct and indirect effects, herbivores can alter succession, plant species diversity and structural heterogeneity and productivity (Ritchie & Olff 1999). Studies of plants of different taxa show that herbivores can change a variety of characteristics of their host plants that may affect their fitness, including growth, number and size of seeds produced (i.e. Green & Palmblad 1975; Hawthorne & Hayne 1978; Bentley et al. 1980; Gómez 1996). Mammalian herbivores often influence plant communities, either by altering the diversity and abundance of plant species by direct consumption, or as an indirect consequence of physical disturbance caused by herbivory (Platt 1975; Huntly & Inouye 1988; Huntly & Reichman 1994). Bark consumption is also considered as herbivory and, in the Southern hemisphere, it has been related mostly to droughts and appears to serve as an emergency water resource (Baxter & Hansson 2001).

This study focuses on the interaction between cuises (*Microcavia australis* Geoffroy & D'Orbigny -Rodentia, Caviidae-) and the creosote bush (*Larrea cuneifolia* Cav. –Zygophyllacea-). Creosote bush is a widespread and ecologically dominant evergreen shrub present in the Monte Desert of Argentina. Because of its abundance and long-lived leaves, it can be regarded as a highly predictable resource in both time and space (Barbour et al. 1977; Rundell et al. 1994). However, despite the availability of creosote bush, herbivory is relatively limited due to the presence of a resinous compound that coats the leaves and stems, which is known to produce toxic effects in laboratory rats and many arthropods (Rhoades & Cates 1976). In South America, creosote bush is consumed by only a few mammal species. Rodents of the genus *Ctenomys* (Mares & Hulse 1977; Borruel et al. 1998) and cuises feed on the leaves, branches and bark of creosote bush (Monge et al. 1994; Campos 1997; Borruel et al. 1998; Campos et al. 2001). The cuis is a diurnal, herbivorous caviomorph rodent widely distributed in Argentina (Cabrera 1953; Tognelli et al. 2001) which reaches high densities in arid zones like the Monte desert (Borruel et al. 1998). It lives in colonies and locates its burrow systems under vegetation exhibiting a weeping structure (Tognelli et al. 1995).

In this study, we explored the influence of spatial variation in herbivory by cuises on the survival and reproduction of creosote bush plants. Within this framework, we examined the effect of gnawing by cuises on creosote bush branches and addressed five specific questions: 1) Is branch damage greater on branches with smaller diameter? 2) Is branch damage greater near cuises colonies than further away? 3) Is there a correlation between level of damage and branch condition? 4) How does damage by gnawing affect flower and fruit production? 5) How does damage by gnawing affect branch survival?

METHODS

The study was conducted in the Ñacuñán Man and Biosphere Reserve, located in the central-western part of the Mendoza Plain (34º02' S; 67º58'W), 200 km southeast of Mendoza, Argentina. The Reserve is in the Monte phytogeographic province (Morello 1958) and comprises approximately 13000 ha of xerophytic vegetation. The climate is semiarid with a long-term average annual rainfall of 322 ± 103 mm (SD, range 192-533; n = 17 yrs), concentrated in the summer months (November to March; mean = 235.22 ± 89.5 mm) (Campos 1997). Mean daily temperatures are lower than 10ºC in winter and above 20ºC in summer. Plant measurements were taken from a scrubland dominated by *L. cuneifolia* associated with other perennial shrubs such as *Lycium chilense* Miers ex Bertero, *Atriplex lampa* Gill. ex Moq., *Condalia microphyla* Cav. and *Capparis atamisquea* Miers ex Hooker et Arnott (Roig 1971).

Creosote bush branches were recorded for the first time and identified with metal tags in 1995. The presence of gnawing by cuises on creosote bush plants is not likely to occur every year, and is restricted to areas of animal activity. Gnawing can be recognized by removed pieces of bark, because cuises never cut branches off these plants. Branch condition was monitored in winter 1996 and summer and autumn 1997. Reproductive success, estimated as the number of flowers and fruits, was assessed only during the summer and autumn of 1997 because creosote bush plants in the study area did not reproduce during 1996.

In 1995, in order to assess the relation between branch diameter and the probability of being damaged, we randomly sampled 98 damaged and 48 undamaged branches. Differences between the two groups were tested with a Student´s t-test.

In order to assess the effect of gnawing on reproductive success after the reproductive season of 1995 (in late spring), we randomly selected 133 branches of similar diameter (78 recently gnawed by cuises and 55 undamaged branches that served as controls). For both groups, the following data were recorded for each branch of creosote bush plants: a) distance to the nearest active cuis burrow (only in 1995), b) proportion of the total perimeter gnawed (only in 1995), c) estimation of the overall condition (in 1995 and 1997), and d) number of buds, flowers and fruits produced (in 1997). Branch condition was recorded based on the amount of new leaves and sprouts present. Branches were categorized as: 1 = dead (no buds, no leaves, dead stem); 2 = poor (no buds, no leaves, live stem); 3 = good (1-3 buds, few leaves); 4 = very good (4 or more buds, numerous leaves). The data on dead branches was also used to perform survival analysis.

To test for correlations between the level of damage and distance to colonies, and between damage and branch condition at the end of the study (in 1997), we performed Spearman rank correlations (Siegel & Castellan 1988). Correlations were made between the percentage gnawed of the total branch perimeter, the condition, and the distance to the nearest burrow.

To determine whether differences in bud, flower and fruit production existed among damage levels, we performed an ANCOVA test. We used the percentage of total branch perimeter gnawed as the independent variable (divided into three categories according to the percentage of the perimeter gnawed: 1 = 0 - 40%; 2 = 41 - 70%, and 3 = 71 - 100%), branch diameter (log-transformed) as a covariant, and the number of buds, flowers, and fruits (all log-transformed) as dependent variables. As branches on the same plant are not independent, a variance-covariance matrix was incorporated including correlations among non-independent branches (Littel et al. 1996).

To assess the effect of gnawing on branch survival we conducted a two-group survival analysis. The effect of the factor "proportion gnawed of the total branch perimeter" (categorized as: high = more than 50% of the branch perimeter gnawed, and low = equal to or less than 50% of the branch perimeter gnawed) on the survival rate of branches in 1997 was compared using Cox's F test (Statistica 6.0; Zar 1999).

RESULTS

The mean diameter of damaged branches (8.05 mm, $SE = 0.3$, range = 3.7 - 18) was significantly lower than that of undamaged branches (13.06 mm, $SE = 1.29$, range = 4.5 - 32, $t = -4.9$, $P < 0.00001$). Also, a significantly negative correlation was found between the proportion of branch perimeter gnawed and distance to active burrows ($r_s = -0.26$, $P < 0.002$, $n = 133$).

At the beginning of the study only four branches were found in the worst condition, versus 39 branches in that category at the end of the study. All of these branches had been gnawed upon by cuises.

None of the undamaged branches worsened their condition during the length of the study (all 55 undamaged branches identified remained in conditions 3 and 4). Branch condition was significantly and negatively correlated with the proportion of total perimeter gnawed ($r_s = -0.68$, $P < 0.000$, $n = 121$).

Reproductive parameters were significantly different among the three levels of damage. Branches with a low percentage of the perimeter gnawed (0 - 40%) had a significantly higher number of buds, flowers and buds and flowers combined (Table 1).

Table 1. Mean number (± SE) of buds (*n* = 50), flowers (*n* = 28), and fruits (*n* = 43) at the three levels of branch damage. Results of ANCOVA test. Letters that differ within a row indicate significant differences according to the post ANCOVA.

Tabla 1. Medias (± ES) de los números de pimpollos, flores y frutos correspondientes a los tres niveles de daño de las ramas. Resultados de la prueba ANCOVA. Las letras indican las diferencias significativas según el análisis post ANCOVA.

	Damage level			
	0 - 40%	41 - 70%	71 - 100%	*p*
Buds	52.30 (± 19.9) a	6.43 (± 2.70) b	5.00 (± 2.06) b	0.01
Flowers	11.46 (± 3.76) a	1.00 (± 0.62) b	0.56 (± 0.32) b	0.03
Fruits	16.50 (± 7.17)	1.57 (± 0.72)	0.88 (± 0.41)	0.14
Flowers and buds	63.76 (± 27.01) a	7.43 (± 3.18) b	5.56 (± 2.45) b	0.009
Branch diameter	9.03 (± 0.56)	7.87 (± 0.67)	7.16 (± 0.34)	

As for the factor proportion gnawed of the branch perimeter, we found a significant difference between the rate of survival of branches with a high proportion of their perimeter gnawed (more than 50% of the branch perimeter gnawed), and branches with a low proportion of their perimeter gnawed (equal to or less than 50% of the branch perimeter gnawed; Cox's F test: F [10, 68] = 2.757; $P < 0.001$).

Discussion

In general, gnawing by cuises negatively affects creosote bush. The results of this study reveal that cuises significantly affect the condition, production of reproductive structures, and survival of branches. The likelihood of being gnawed upon is higher in plants growing closer to cuis colonies and for branches of a smaller diameter. Thus, branches might reach a certain diameter (> 18 mm), above which they would be less likely to be damaged by cuises ("size refugium" *sensu* Myster & McCarthy 1989). In this respect, we wonder whether cuises prefer smaller branches because of their tenderness, nutritive value or lower contents of secondary compounds.

The effect of herbivory by cuises can then range from reducing plant fitness to the loss of a whole branch or branches. Creosote bush has a particular architecture with branches that ramify at ground level and grow outwards, like an inverted cone. This type of plant architecture may be very important for coping with different herbivores. This species, as many other plants, has a metameric construction in which each branch can be regarded as an individual metamer or a quasi-autonomous independent unit (Watson 1986). In such plants, resources can flow more freely within morphological units than between them, a phenomenon that has been termed sectoriality (Watson 1986). Sectoriality may influence a plant's ability to tolerate tissue loss (Marquis 1996). Without modular construction, loss of terminal growing points due to herbivory will lead to the death of the plant (Marquis 1996). Thus, in creosote bush, the presence of several branches per plant may compensate for the reduction in reproductive organs, or even for the complete loss of a branch.

Another finding of our study is that the likelihood of being gnawed upon is higher in plants growing closer to cuis colonies. This may be a consequence of the fact that cuises concentrate most of their activities near their burrow systems, feeding on nearby plants (Rood 1970). Other studies also have found that the impact of mammalian herbivores is inversely related to distance from burrows or from plant cover (Fuentes et al. 1983; Longland 1991; Swihart 1991; Swihart & Picone 1991; English & Bowers 1994). This foraging behavior can affect plant distribution whenever plants are selected nonrandomly by species or spatial position, by creating local gradients and mosaic patches of vegetation (Ostefld et al. 1994). In a previous study (Tognelli et al. 1999), we found a similar pattern in the effect of gnawing by cuises on the tree *Geoffroea decorticans* Gill. ex Hook. et Arn., which led us to speculate that predation risk may be a determinant of this feeding behavior of cuises. This study shows the spatial heterogeneity of herbivory by cuises and their effect on the survival and reproduction of creosote bush branches.

ACKNOWLEDGEMENTS

C. Campos, S. M. Giannoni and C. Borghi are CONICET (National Council for Science and Technology) researchers. M. Dacar and S. Monje helped us during the fieldwork and N. Horak assisted with the English version. Anonymous reviewers and the editor greatly improved the manuscript with thier comments. This research was partially supported by CONICET through Grants # 3638/92 and Agencia de Promoción Científica y Tecnológica (PICT 03281; PICT 11768).

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