

Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe

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Abstract. *Field observations while traveling through the Patagonian steppe over the past 15 years have left me with a clear impression of how well defended many of the plants are against herbivory. The objectives of this paper are to question the prevailing hypothesis that the evolutionary history of herbivory in Patagonia has been short and to ask if there is any evidence to support an alternative hypothesis of a long evolutionary history. The analysis is entirely speculative based upon personal observations, discussions with colleagues and a diverse selection of material from the literature. My conclusion from this analysis is that there is at least enough support for an alternative hypothesis to justify proposing it. Furthermore, the long evolutionary history hypothesis is consistent with observations of frequent herbivore defenses among the dominant plants and relative resistance of upland sites to large negative effects of 100 years of herbivory by sheep.*

Introduction

Between April 26 and May 8, 1998 I participated in a field mission to Patagonia sponsored by the World Bank through a project with DHV Consultants. The objective of the mission was to provide an international perspective on the state of desertification of Patagonian rangelands. My specific role was to provide that perspective with respect to similar rangelands in North America. The observations that I made during this trip to Patagonia were the impetus for this short paper.

Field observations

April 27, 1998. We stopped along the road between Comodoro Rivadavia and Sarmiento and walked out into the steppe to look at a site on which *Festuca argentina*, a toxic grass, was the dominant species. Among the spiny shrubs and the unpalatable *Stipa speciosa* we also found a few individuals of the palatable grass *Poa ligularis*. The physiognomy of the site was that of a shrub-steppe with a very large aboveground biomass of grasses. The site seemed to be in good condition based upon the large size of the few palatable grasses. Having had my expectations of temperate shrub-steppe ecosystems conditioned by the Great Basin of the United States, which occupies a similar climatic zone as the Patagonian steppe but has fewer spiny shrubs and a larger number of palatable grasses, I began to wonder about the origin of the fine array of defenses against herbivory that most of the plants at this site possessed. I recalled a trip to Saudi Arabia on which I was similarly impressed by the armor displayed by the plants to defend themselves from the enormous grazing pressure to which they had been subjected over the past several million years and continue to be subjected today.

April 28, 1998. After visiting several small farms in the morning, we left Sarmiento on our way to Perito Moreno. Between Colonia Las Heras and Perito Moreno, we stopped at a site that had been abandoned from sheep production and, as a group marveled at the size and number of individuals of the palatable grasses at this site. Despite the fact that there were a relatively large number of

individuals of palatable grasses at this site compared to other sites we had seen, I was very impressed by the small proportion of the total aboveground biomass that is accounted for by palatable species. *Stipa speciosa* provided much of the aspect of the site giving it a very 'grassy' look. In the North American bunchgrass steppe, a site with this much biomass of bunchgrasses would be dominated by *Pseudoroegneria spicata*, *Festuca idahoensis*, one or more of several species in the genus *Shpa*, *Pascopyron smithii* and/or *Elymus lanceolatus*, all of which are palatable. As I inspected the other plants, I touched the spines of *Nassauvia glomerulosa* and was amazed by their length, thickness and sharpness. I took pictures of *Schinus polygamous* and *Berberis heterophyla*, thinking they would provide terrific examples of plants with spines as a defense against herbivores for my grassland and shrubland course at Colorado State University.

Closer to Perito Moreno we stopped to look at eroded mallines (sub-irrigated meadows often with a well developed peat layer), not just one, but many of different sizes and degrees of degradation. At one of our stops, in the midst of a discussion about degradation of Patagonia and desertification, I was unable to keep from noticing how subtle the effects of grazing were on the uplands compared to the mallines. Everywhere I looked on the uplands, I saw *Stipa speciosa* and the full complement of shrubs I had come to expect. Furthermore, as I wandered away from the group, and began looking carefully at the upland vegetation I found the palatable grasses. Not large individuals growing in the spaces between the shrubs as we had seen at the last stop but small ones, appressed to individuals of *Stipa speciosa* or underneath the armor of *Schinus polygamous*. Despite the evidence from the mallín of heavy past grazing pressure, it appeared that the full complement of species was still present on the uplands and that the physiognomy of the site had been changed very little. This observation made me think about how lucky we are that such a small amount of the biomass of the steppe is palatable to sheep. This then lead to thoughts about how well adapted the plant community is to withstand herbivory.

These two journal excerpts from my trip to Patagonia in the Fall of 1998 are representative of the reactions I have had on previous trips. Over the time I have been visiting Patagonia, I have been consistently amazed by how unfriendly the plants are to herbivores. To put this idea in the terms I used in my journal and those most often used by ecologists; it is amazing how well adapted the Patagonian steppe plant community is to withstand herbivory. The difficulty I have had in the past with this idea is that it contradicts the prevailing view. Daniel Milchunas, Osvaldo Sala and I constructed a conceptual model which we claimed explained differences in how plant communities world-wide respond to herbivory (Milchunas et al. 1988). In our analysis of the data that went into the model for Patagonia, we made two important assumptions. First, we assumed that most of the herbivores in Patagonia were extinguished by the most recent glacial event and second, that the past 10,000 years in the evolution of the plants has been in the absence of heavy selection pressure by a generalist herbivore. The data to support the first assumption are quite convincing (Markgraf 1985). We assumed that since the first assumption was valid that the second assumption was a clear logical consequence. My objective for this paper is to provide some speculation about why our second assumption may be incorrect.

The conceptual model

The key features of the Milchunas et al. (1988) model are a set of ideas related to the similarity of selection pressures exerted by a productivity gradient and by herbivory. In the absence of herbivory, the selection pressures to which plants are subjected along a productivity (precipitation) gradient change from competition for belowground resources at the dry end of the gradient to competition for light at the wet end of the gradient. Under dry conditions, competition for belowground resources should select for plants with extensive root systems and limited canopy development (short plants) while competition for light should select for extensive canopy development (tall plants). Herbivory, by contrast, always selects for short individuals. Combining the two selection pressures produces some interesting situations. At the dry end of the gradient, both

forces select for similar morphologies and physiologies: low growing plants that are able to withstand a high turnover in aboveground plant parts. At the wet end of the gradient, the two forces select for different plant attributes. Using these ideas, Milchunas et al. (1988) proposed that one can understand the response of a plant community to grazing by considering its position along the productivity gradient and understanding its evolutionary history of herbivory.

Establishing the location of a site on the productivity axis is straightforward if one assumes a linear relationship between mean annual precipitation and aboveground net primary production (Walter 1971, Lauenroth 1979, Sala et al. 1988, Paruelo et al. 1998). Where a plant community lies along the evolutionary history axis is a much more difficult issue; the most common evidence is either anecdotal or circular. By circular, I mean that the length of the evolutionary history of a community is judged by the evidence of adaptations of the plant community to herbivory.

In the Milchunas et al. (1988) paper, we identified a number of locations world-wide that we considered to be representative of the four extreme conditions: low production-short evolutionary history; low production-long evolutionary history; high production-short evolutionary history and high production-long evolutionary history. Our type examples for the low production-short evolutionary history case were the Great Basin of the western United States and Patagonia. The Great Basin example is fairly clear. Most of the large herbivores in this region went extinct during the last glaciation, and for the past 10,000 years the plant species in the region have evolved in the absence of a heavy selection pressure by a generalist herbivore. While there are some plants that have characteristics that could be interpreted as adaptations to grazing, most do not. Essentially all of the grasses are palatable and sensitive to grazing. The introduction of cattle into the region in the last half of the 19th century had a very large negative effect on many plant communities, from which they have not yet recovered (Miller et al. 1994). The negative impact of livestock grazing in the Great Basin of the U. S. has been compounded by the introduction of a large number of exotic plant species, several of which have been enormously successful (Young et al. 1972, Miller et al. 1994).

Were we correct in including the Patagonian steppe in the same category as the Great Basin of the United States? There appears to be abundant evidence that the plants have well developed defenses against herbivory. Is there any information about past populations of herbivores?

Analysis of the Patagonian steppe

South America is widely recognized as having a small number of species of mammalian herbivores (Keast 1972). Over the past several thousand years, there were only four herbivores in Patagonia and only one, the guanaco (*Lama guanicoe*), was present in large numbers (Franklin 1982). Guanacos are modest sized animals averaging approximately 120 kg live weight (Franklin et al. 1997). They are generalist herbivores, and their diets show a high degree of overlap with diets of both sheep and cattle (Bovino and Pelliza 1991, Somlo 1997). An interesting and important characteristic of camelids is a highly efficient nitrogen recycling system which allows them to consume a larger amount of low quality forage than either sheep or cattle (Schmidt-Nielsen et al. 1957, Livingston et al. 1962). This, in addition to a highly efficient water balance, would allow guanacos to inhabit portions of the upland steppe that have too low a forage quality and are too dry for sheep or cattle.

While current populations of guanacos in Patagonia are low (< 546,000; Franklin et al. 1997), Raedeke (1979), using livestock numbers as a basis, estimated that there were 30-50 million guanacos in southern South America at the time of arrival of Europeans. Even if we accept this number as correct, it is impossible to know how many were in Patagonia. An indication of both the potential of Patagonia to support guanacos and the potential of guanacos to increase under favorable conditions is provided by the change in the numbers of guanacos on 2000 km² in Tierra del Fuego in Chile between 1977 and 1993 (Franklin et al. 1997). As a result of protection from hunting, guanacos increased from a density of 2.7 per km² in 1977 to 8.2 per km² in 1993. Density peaked at 10.2 guanacos/km² in 1992. These densities were in the presence of 50 sheep/km² and 3 cattle/km².

Using a conversion of 2.5 sheep per guanaco (Raedeke 1979), I estimated that the total potential density of guanacos could have been 28-30 guanacos/km². A density of 30 guanacos/km² over the 730,000 km² of Patagonia in Argentina would mean 22 million guanacos.

How much forage would 30 guanacos/km² require? If we assume that guanacos are similar to many other ruminants and require 3 % of their body weight in forage daily, and to be conservative we assume that the entire population is made up of adults that weigh 120 kg, 30 guanacos/km² would require an average annual forage production over each km² of 46 g/m². Is this amount of annual forage production possible? Fernandez et al. (1991) reported five years of annual aboveground net primary production for an upland site at Río Mayo in Chubut Province. Annual precipitation over the five years ranged from 55 to 190 mm and annual aboveground net primary production ranged from 21 to 75 g/m². These data suggest that 30 guanacos/km² would be possible at Río Mayo, assuming that guanacos could consume a large fraction of the annual production. Since they may be ten times more efficient in recycling nitrogen to their rumen than sheep are (Schmidt-Nielsen et al. 1957, Livingston et al. 1962), this may not be a bad assumption. A more significant restriction on the population size would be the ability of the ecosystem to sustain such a large removal of annual net production. Milchunas and Lauenroth (1993) reported consumption by grazing animals as a percentage of annual aboveground net primary production for grasslands and shrublands worldwide. The average for 104 grassland sites was 44% and for 35 shrubland sites was 55%. If we apply the shrubland value to the Río Mayo data, this suggests that 12 to 41 g/m² could be consumed by grazing animals. These calculations suggest that the range in density that could be supported at Río Mayo would be 8-27 guanacos/km².

Conclusions

While we will never know how abundant guanacos were in Patagonia over the past 10,000 years, it seems to me that there is ample reason to speculate that there could have been sufficiently large populations to have consumed a large fraction of the annual aboveground net primary production and thus created a substantial selection pressure for the plants to develop defenses against herbivory. This selection pressure would have been complementary to the selection pressure created by the dry windy environment (Coughenour 1985, Milchunas et al. 1988). Both herbivory and aridity would have selected for similar plant characteristics. One of the appealing things about the idea that there were sufficient guanacos to exert significant selection pressure on the evolution of plants in the steppe is that it provides an explanation for the current array of herbivore defenses. Furthermore, it explains some of the important differences between the North American bunchgrass steppe and the Patagonian steppe. In terms of the Milchunas et al. (1988) model, it would move the Patagonian steppe from an example of a low productivity environment with a short evolutionary history of grazing, which at the moment it shares with the North American bunchgrass steppe, to one with a long evolutionary history of grazing, placing it in the same category as the North American shortgrass steppe. The Milchunas et al. (1988) model predicts that plant communities with a long evolutionary history in a low productivity environment should respond to grazing pressure gradient with small decreases in plant species diversity. While there are not many data relevant to this issue for the Patagonian steppe, the available data suggests a small change in diversity with grazing (Schlichter et al. 1978). Moving the location of the Patagonian steppe in the Milchunas et al. (1988) model has a number of consequences: it should change the way ecologists think about the steppe; it should modify conclusions about desertification as a result of historical grazing; and it should influence the kinds of management strategies that are developed for the steppe.

Acknowledgments. In formulating the ideas for this paper I have benefitted from discussions with I.C. Burke, O.E. Sala, D.G. Milchunas, J.M. Paruelo, M.R. Aguiar, V.A. Deregibus, P. Borrelli, L. t'Mannetje, N. Beck, and B. van Barneveld. I.C. Burke, J.M. Paruelo, O.E. Sala and P.B. Adler made many important suggestions on a draft of the manuscript. S. Diaz and G. Rush provided many helpful review comments.

Preparation of the manuscript was partially funded by a grant from the National Science Foundation (DEB-9350273) and a grant from the Colorado Experiment Station (157661).

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Received: July 14, 1998

Accepted: March 17, 1999