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Wild guanacos as scapegoat for continued overgrazing by livestock across southern Patagonia

Andrea Marino[1] | Victoria Rodríguez[1] | Natalia M. Schroeder[2]

[1]Instituto Patagónico para el Estudio de los Ecosistemas Continentales, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

[2]Instituto Argentino de Investigaciones de Zonas Aridas, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

Correspondence
Andrea Marino
Email: marino@cenpat-conicet.gob.ar

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Abstract

1. In a recently published paper, Oliva et al. concluded that domestic grazing pressure across Patagonian rangelands approached carrying capacity due to decades of stock adjustment, but that guanaco overpopulation may have altered that balance. The authors argued that unless guanaco numbers are controlled, they will reduce forage available for domestic stock and will negatively affect rangelands. We consider that the herbivore-stock analysis presented is inaccurate and deserves revision, and that the stated conclusions lack empirical support.
2. When the spatial distribution of herbivores is accounted for in the Oliva et al. analysis, domestic stock is far above carrying capacity, indicating that domestic overgrazing continues.
3. Theoretical and empirical evidence on bottom-up regulation and competitive exclusion challenges the supposed guanaco overpopulation and the hypothetical reduction of forage available for livestock.
4. Even if guanaco numbers are reduced, grassland degradation and production losses will continue because their main drivers, domestic overstock and heterogeneous grazing, are still operating.
5. *Synthesis and applications*. Oversimplified models with poor ecological insight can lead to erroneous conclusions and misguide management decisions. The incorrect inference that Patagonian domestic stock is adjusted to carrying capacity could help to consolidate current domestic overgrazing by reducing incentives to improve livestock management practices. Regarding guanacos, a controversial species in an unfavourable context, control-oriented harvest without a clear justification threatens populations' viability and genuine attempts of productive diversification. Addressing relevant ecological processes, such as niche partitioning, competitive exclusion and population regulation, is essential to correctly assess joint carrying capacity in multi-herbivore systems, as well as to identify the true factors driving degradation processes and to optimize rangeland use on a sustainable basis.

KEYWORDS
carrying capacity, Guanaco, livestock, multi-herbivore systems, Patagonia, rangelands management, wild-herbivores

1 | INTRODUCTION

Recently, an article titled 'Remotely-sensed primary productivity shows that domestic and native herbivores combined are overgrazing Patagonia' was published in the Journal of Applied Ecology. In this article, Oliva, Paredes, Ferrante, Cepeda, and Rabinovich (2019) compared their carrying capacity (CC) estimates with wild and domestic herbivore numbers. The authors concluded that after decades of stock adjustment, total domestic grazing pressure came close to CC, but in the Chubut and Santa Cruz Provinces, guanaco *Lama guanicoe* populations may have altered the balance in the last two decades. Finally, the authors claimed that, unless guanaco numbers are controlled, forage available for domestic stock will be reduced, increasing herbivore mortality, and rangeland health will be negatively affected. We share the authors' concern about the degradation of the Patagonian grasslands but we consider that the herbivore-stock analysis presented is inaccurate and that speculations on the relative impact of guanacos contradict both ecological theory and empirical evidence. The aim of this note is to show that available information on the spatial distribution of the herbivores defies the basic assumption upon which the Oliva et al. modelling relies, that is that each species had exclusive use of the land/forage. When spatial distribution of both guanacos and livestock is included in the analysis—assuming the reliability of the estimates of consumable forage previously computed—the resultant scenarios are substantially different, calling into question the stated conclusions. We present a brief summary of available evidence that challenges Oliva et al.'s statements on the corresponding roles of guanacos and livestock in the current crisis. Finally, we suggest critical ecological aspects to be addressed that may help to improve the CC assessment in multi-herbivore systems.

2 | DOMESTIC STOCK NUMBERS AND FORAGE FAR FROM EQUILIBRIUM

According to Table 3 and Animal Unit (AU) equivalents from Oliva et al. (2019), the Chubut Province was able to support 644,000 AU and Santa Cruz 474,000 AU. Domestic stock reported were 744,210 (referred to 208,328 km^2) at Chubut and 448,620 AU (referred to 222,636 km^2) at Santa Cruz. According to these numbers, the authors concluded that domestic stock would be slightly over (Chubut) or below CC (Santa Cruz), having reached a near equilibrium with forage resources after six decades of overgrazing and forced stock adjustment, but that guanaco numbers are now altering that balance.

However, as stated by Oliva et al., after massive overstocking, the total numbers of livestock within the Chubut and Santa Cruz Provinces had declined by the end of last century since producers were forced to reduce flocks and/or abandon the land. By 2015, at least 30,000 km^2 at the Central Plateau of Chubut (Carcamo, Llanos, & Muñoz, 2016) and more than 100,000 km^2 at Santa Cruz were occupied by abandoned ranches (Oliva et al., 2017). Additionally, the government in Santa Cruz converted 2,764 km^2 of Patagonian steppes into protected areas (https://sib.gob.ar) without livestock. These facts clearly refute the main assumption on which the whole approach of the analysis is based ('each herbivore had exclusive use of the land'), and question the validity of the stated conclusions. For example, regarding Santa Cruz, most of the 100,000 km^2 of abandoned lands (about 400 ranches) is located in the Central Plateau biozone (Andrade, 2012), changing the estimate of the actual livestock excess according to the methods presented in the paper. The CC reported for Santa Cruz for 2015 was 474,000 AU. However, subtracting the consumable forage that corresponds to the 102,764 km^2 of the Central Plateau biozone without livestock, which was reported to produce 67 kg DM^{-1} ha^{-1} (215,160 AU when converted to CC units), leaves only 258,840 AU for the rest of the area where livestock is held (119,872 km^2). Consequently, if by 2015 the total domestic stock for the entire Santa Cruz Province was 448,620 AU, in the area effectively occupied by livestock and under the Oliva et al. approach, our reanalysis shows that there is a livestock excess close to 73% and consequently overgrazing by livestock is not only present but at likely unsustainable levels (Table 1).

The same procedure could be applied to Chubut (Table 1), which was already overstocked with domestic herbivores in the original analysis. This result shows an increase in livestock excess from 15% to 28%. Therefore, there is no balance between domestic stock

TABLE 1 Area, carrying capacity (CC), domestic stock and domestic overgrazing for areas with and without livestock at Santa Cruz and Chubut Provinces for 2015, based on values reported by Oliva et al., 2019. Domestic overgrazing = 100 × (domestic stock − CC)/CC

Province	Area (km^2)	CC (AU)	Domestic stock (AU)	Domestic overgrazing (%)
Santa Cruz				
Area with livestock	119,872	258,840	448,620	73
Area without livestock	102,764	215,160		
Total	222,636	474,000	448,620	
Chubut				
Area with livestock	179,031	582,660	744,210	28
Area without livestock[a]	29,297	61,340		
Total	208,328	644,000	744,210	

[a]To compute this area, we considered only 50% of the area of sub-occupied ranches according to Carcamo et al. (2016).

and forage resources as the authors claimed, but instead a combination of degraded areas that were abandoned and areas that are still under high grazing pressure by livestock, presumably ongoing the same degradation processes. The magnitude of the differences between Oliva et al. and our results warrants a detailed revision of the relationships between herbivore numbers and forage availability across pertinent spatial scales in order to correctly assess risks and derive sound management recommendations.

3 | GUANACO DISTRIBUTION, LIVESTOCK GRAZING HETEROGENEITY AND FORAGE ACCESS

Regarding guanacos, to assume that they have equal access to forage resources available to livestock contradicts the vast empirical evidence currently available. The Oliva et al. approach overlooks essential ecological concepts, such as competitive exclusion and niche partitioning, and the basic principles of domestic-wild ungulate interactions and potential for competition. The *Competitive Exclusion Principle* states: 'if two competing species coexist, then they do so as a result of niche differentiation. If, however, there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other' (Begon, Townsend, & Harper, 2006). Guanacos were historically the dominant herbivores across South American arid ecosystems, with a population estimated at 30–50 million individuals until European colonization (Raedeke, 1979). After sheep were massively introduced into Patagonia, guanaco numbers decreased sharply due to direct competition, habitat degradation and over-hunting. Population decline was so intense that in 1993 CITES demanded that Argentinean authorities cease commercial harvest (Baldi et al., 2006). Remaining guanacos persisted in marginal habitats or protected areas. Since that time, a growing body of evidence supporting the hypothesis of livestock competitively excluding guanacos has been gathered. Regarding regional or landscape scales, the inverse relationship between sheep and guanaco densities has been reported in numerous studies, with sheep occupying the most productive areas, whereas guanacos are displaced to marginal habitats (Baldi, Albon, & Elston, 2001; Pedrana, Bustamante, Travaini, & Rodriguez, 2010). According to the results of the abundance survey (Bay Gavuzzo et al., 2015) used by Oliva et al., population density at the Central Plateau biozone of Santa Cruz was 6.62 guanacos/km^2 where, as previously mentioned, 102,764 km^2 are free from livestock. Hence, at least 680,298 guanacos, 50% of the total 1,359,000 guanacos estimated for Santa Cruz, would be occupying livestock-free abandoned ranches. The proportion of the guanaco population of Santa Cruz occupying the livestock-free zone increases up to 74% if the Travaini el al. (2015) peer-reviewed results are considered. Therefore, instead of each herbivore having exclusive use of the land as the authors assumed, there is a clear conditioning on both guanacos and livestock distribution and hence on their access to total available forage.

The hypothesis of the remaining guanaco population (after accounting for the proportion occupying abandoned ranches) using livestock-destined forage is not supported by available studies at lesser spatial scales either. In addition to the generalized overestimation of CC by Patagonian ranchers (Golluscio, Deregibus, & Paruelo, 1998), livestock grazing heterogeneity resulting from habitat and diet preferences and/or physiological restrictions has been pointed out as a major cause of grassland degradation and livestock poor performance (Tanaka et al., 2007). In southern Patagonia, land subdivision at the end of the XIX century and subsequently paddock layout were based on geometric principles rather than ecological considerations, and landscape heterogeneity was ignored in the process (Ormaechea, Peri, Cipriotti, & Distel, 2019). Due to livestock concentration in the most preferred places, paddocks often show a combination of highly degraded and sub-utilized areas (Cingolani, Noy Meir, Renison, & Cabido, 2008; Valentine, 1947). Distribution of water sources and paddock size is typical determinants of domestic grazing heterogeneity (Oñatibia & Aguiar, 2018). Sub-utilized, less impacted sites have been identified as wildlife refuges, particularly for species whose habitat has been essentially modified by domestic grazing or that are out-competed by livestock (Fuhlendorf & Engle, 2001; Saba, Perez, Cejuela, Quiroga, & Toyos, 1995). Consistently, when assessing their spatial distribution within livestock ranches, guanacos were mostly found in areas away from water sources where sheep are rarely observed (Rodríguez, Marino, & Schroeder, 2018; Saba et al., 1995), or restricting their distribution to other areas avoided by domestic herbivores, such as steep terrain (Iranzo et al., 2013) or far from human settlements (Schroeder et al., 2013). Finally, the paddock area was the best predictor of guanaco abundance across Península Valdés, with increasing encounter rates in larger ones (Nabte, Marino, Rodríguez, Monjeau, & Saba, 2013), according to the predicted wildlife-refuge effect. These results, consistent across different spatial scales, support the hypothesis that guanacos can only occupy areas where they are able to exploit forage that is out of reach of livestock. In areas where niche differentiation is precluded by habitat features and the sheep realized niche overlaps the guanaco fundamental niche completely, guanacos are virtually absent, as was confirmed across the southern grasslands of Península Valdés (Baldi, Campagna, & Saba, 1997; Nabte et al., 2013). Raedeke (1979) came to the same conclusion at Tierra del Fuego 40 years ago, including other niche dimensions. Additionally, ecological release (Begon et al., 2006) of guanacos after sheep removal has been documented, confirming competitive exclusion by a process-oriented approach (Burgi, Marino, Rodríguez, Pazos, & Baldi, 2012).

According to the competitive exclusion process described above, that seems to have shaped guanaco distribution and abundance since livestock introduction, it is certainly unlikely that guanaco populations will suddenly start growing to reduce forage available for domestic stocks, since guanacos do not seem capable of out-competing livestock for forage resources. It is more appropriate to hypothesize that, as guanacos are able to consume low quality forage and inhabit degraded areas that can no longer sustain sheep production, their populations have grown during recent years by reoccupying the vacant areas left after livestock production ceased. To overlook niche partitioning in considering guanaco-livestock co-occurrence wastes opportunities for optimizing rangeland use by the implementation of diversified production schemes, including wild and domestic herbivores, and taking advantage of their corresponding adaptations.

4 | POPULATION REGULATION AND GUANACO OVERGRAZING RISK

The (debatable) lack of predators emerges recurrently when ranchers demand extractive management to reduce the supposed guanaco overpopulation, often arguing that no herbivore species can be regulated in the absence of predation hence disregarding 60 years of ecological debate on the relative importance of top-down (mediated by predators) versus bottom-up (food shortage) processes in shaping herbivore dynamics (Kay, 1998). To date, it is generally accepted that bottom-up processes are the basic rule, particularly for the largest species, whereas populations of smaller herbivores might be regulated by predation, food shortage or a combination of both (Hopcraft, Olf, & Sinclair, 2010). The guanaco's natural predator is the puma *Puma concolor* which is a territorial, lone predator with a generalist diet, whose ability to regulate prey species at medium-high density, including guanacos (Novaro & Walker, 2005), is restricted by its own social organization and feeding habits (Hornocker, 1970). Therefore, from a predator traits perspective, it seems unlikely that the Patagonian steppe has evolved under the effects of top-down regulation.

Errington (1956) stated that, compared to the basic role of territoriality, predation has a secondary role as a regulating agent of prey populations. In contrast to non-territorial species that can overpopulate an area for long periods and sometimes lead to habitat degradation, guanacos do exhibit an outstanding territorial behaviour resulting from resource defence polygyny (Franklin, 1983). Under regular dispersal conditions such as those found across most Patagonian rangelands, intense relationships among forage quality and quantity and territorial behaviour result in the limitation of population density below the numbers predicted by actual forage availability (Franklin, 1983; Marino, Rodríguez, & Pazos, 2016).

Therefore, under the top-down regulation hypothesis, unmanaged guanaco populations without significant predation would grow excessively, overgrazing grasslands, which would ultimately induce population collapse. An alternative hypothesis consistent with available knowledge is that guanaco-vegetation dynamics have evolved by a bottom-up process mediated by resource defence, in which the interaction between behavioural traits and forage availability results in the active adjustment of population density, promoting relatively moderate and homogeneous grazing, regardless of predation intensity. Density limitation below CC resulting from resource defence weakens the Oliva et al. prediction of unmanaged guanacos overshooting K in poor years and stresses the need of direct evidence of guanaco overgrazing to validate this affirmation.

Among various empirical examples supporting the bottom-up alternative, a protected area located at Chubut showed that, after a substantial vegetation recovery following sheep removal and in spite of the growth of the guanaco population reaching the highest herbivore densities across the zone, no evidence consistent with vegetation deterioration has been found during 10 years of monitoring (Pazos, Rodríguez, & Blanco, 2017), with a stabilized guanaco density below CC assessed in situ by forage harvest (Marino et al., 2016). Other studies have reported contrasting vegetation states, with overgrazed sites intensively used by livestock in the proximity of water sources whilst the sites where guanacos foraged remained well conserved (Saba et al., 1995). It is worthwhile to stress that at the mostly livestock-free Central Plateau of Santa Cruz where the previously stated 50%–74% of the guanacos occur and thus guanaco overgrazing would be expected, a null or slightly positive tendency in greenness has been reported for the 2000–2014 period (Gaitán, Bran, & Azcona, 2015). Conversely, we are not aware of peer-reviewed scientific studies in which guanacos have been found responsible for vegetation degradation.

For the reasons explained, theoretical and empirical arguments disregard top-down regulation in favour of a bottom-up process mediated by resource defence territoriality. On the basis of plant grazing resistance traits, at present it is accepted that guanacos have been a strong selective pressure in shaping the Patagonian steppe, definitively supporting the bottom-up hypothesis and stressing the role of their vast populations in guanaco-vegetation co-evolution (Adler, Milchunas, Lauenroth, Sala, & Burke, 2004; Lauenroth, 1998). Thus, it seems improbable that guanaco grazing will suddenly become a threat to the integrity of Patagonian grasslands.

5 | CONSERVATION AND MANAGEMENT IMPLICATIONS

Estimating CC in multi-herbivore systems has proven to be a complex matter globally, and it might be impossible to include all relevant aspects within an applied approach. However, in order to make reliable predictions, model assumptions must be coherent with the available empirical knowledge. Even though Oliva et al. acknowledged some of the issues raised above in the discussion section of their paper, the authors omitted these aspects in the initial approach, assumed an unreal scenario and even so derived management recommendations without warning against the limitations of their analysis. Oversimplified methods with poor ecological insight can support erroneous conclusions with decisive political significance, such as livestock numbers being adjusted whilst guanacos are the ones that are endangering the ecosystem balance. Rather than using simple linear combinations of species abundances and body weights, a minimum approach to assess joint CC should also include the distribution of each species and its determinants, taking explicitly into account spatial segregation, diet preferences and any significant seasonal variation in relevant variables. Above all, any method proposed should be supported by direct, field validation of harvest indexes and overgrazing thresholds prior to deriving extractive management recommendations on a controversial native species under a theoretical overpopulation premise. Oliva et al. stated that commercial harvest of native wildlife may guarantee conservation but regarding guanacos, the consequences of commercial hunting during past century call into question this claim. The imminent extractive plans oriented to rapidly reduce guanaco numbers, government attempts to develop new markets for guanaco products, inability to control illegal harvest and the weak Argentinean institutional context bring back the risk of overexploitation on the recently recovered populations and threaten genuine attempts of productive diversification through sustainable harvest or live shearing initiatives. Thus, recommendations on the need of control-oriented harvest of guanacos should be solidly grounded.

As stated, theoretical and empirical evidence does not support the idea of unmanaged guanaco populations jeopardizing grassland integrity or livestock production. However, even if guanacos were eradicated, unless traditional management practices change, the current factors driving land degradation and production losses (i.e. grazing heterogeneity and domestic overstock) would continue operating. Massive economic and political efforts are underway by the Santa Cruz Province and the Federal governments to change current legislation and allow the reduction of guanaco numbers, instead of fostering the improvement of livestock management schemes. A study on landholder perceptions revealed that, although 75% detected heterogeneous grazing in their paddocks, they do not seem to consider it important enough to deserve attention. The study also revealed that the extensive system in South Patagonia continues 'under a scheme of minimal intervention of the landscape, just as in its beginnings' (Ormaechea et al., 2019), with ranchers unable to account for the damaging effects of their own practices (Andrade, 2012). As stated by Ormaechea et al. (2019), unless technology extension institutions start helping landholders and policy makers correctly assess the relative importance of the factors that negatively affect production, it is unlikely that they will be able to overcome the farming crisis and reverse the current land degradation process affecting Patagonian grasslands.

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AUTHORS' CONTRIBUTIONS

V.R. and A.M. conceived the ideas and designed methodology; V.R. and N.M.S. analysed the data; and A.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All the data used in this article are published elsewhere, and therefore, it is already accessible for the public (Bay Gavuzzo et al., 2015; Carcamo et al., 2016; Oliva et al., 2017, 2019; Travaini et al., 2015). The corresponding reports' URLs are included in the reference list.

ORCID

Andrea Marino https://orcid.org/0000-0001-8087-5541

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