

Natural and Social Sciences of Patagonia

Pablo Carmanchahi
Gabriela Lichtenstein
Editors

Guanacos and People in Patagonia

A Social-Ecological Approach
to a Relationship of Conflicts and
Opportunities



Springer

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Chapter 5

Guanaco Predation by Pumas and Its Relationship to Patagonian Food Webs



Emiliano Donadio, Juan I. Zanón Martínez, Pablo Alarcón,
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5.1 Introduction

5.1.1 *Predator–Prey Interactions and Their Importance to Communities and Ecosystems*

Predator–prey interactions represent a fundamental ecological mechanism whose effects reverberate through communities and ecosystems (Terborgh and Estes 2010). Indeed, besides influencing numbers and distribution of interacting species, the effects of predator–prey interactions can extend to lower trophic levels (Schmitz et al. 2000) that potentially enhance populations of other species and their predators (McCauley et al. 2006). Rooted in the *green world* hypothesis (Hairston et al. 1960),

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which predicts that predators limit herbivores and in doing so benefit vegetation, the idea that predators can structure biological communities through indirect effects was first demonstrated by Paine (1966); this work was subsequently corroborated by the remarkable work of Estes and Palmisano (1974) who showed how marine kelp forests persisted where sea otters (*Enhydra lutris*) thrived. This type of indirect interaction between species is broadly termed trophic cascade (Ripple et al. 2016) and has been revealed by numerous experimental and observational studies in a diverse array of aquatic (Strong 1992) and terrestrial ecosystems (Schmitz et al. 2000). In general, these studies highlight the importance of trophic relationships to community structure and ecosystem function. When predator–prey interactions are altered, often via the removal of predators, cascading effects are eroded, and ecosystems commonly transition to states that are simpler than those that initially existed (Terborgh et al. 2010).

Predators can trigger trophic cascades through two non-exclusive pathways: (1) density-mediated trophic cascades arise when predators significantly reduce the numbers of herbivores and, and (2) behaviorally mediated trophic cascades occur when herbivores shift their behaviors in response to the perceived risk of being killed (Schmitz et al. 1997). Although experimental data supports the existence of both pathways in systems involving invertebrates and small vertebrates (Beckerman et al. 1997; Pace et al. 1999; Knight et al. 2005), parallel evidence is missing from systems featuring large carnivores and their herbivore prey (Ford and Goheen 2015; Allen et al. 2017). Still, numerous correlational studies strongly suggest that large predators not only initiate trophic cascades that protect vegetation but also support multiple taxa. Simultaneously, trophic cascades can affect other ecological processes such as scavenger subsidies, nutrient cycling, and disease dynamics (Estes et al. 2011; Ripple et al. 2014). These interactions involving large carnivores and herbivores and the associated cascading consequences have been forged over long periods of coevolution. Thus, their persistence is suspected to be critical in maintaining the integrity and continued balance of ecosystems, including those found across Patagonian landscapes.

Here, we review and synthesize data on guanaco (*Lama guanicoe*) and puma (*Puma concolor*) ecology, emphasizing trophic interactions and guanaco antipredator responses. Subsequently, we frame this information within food-web theory to assess whether guanaco predation by pumas has the potential to trigger a trophic cascade with effects on vegetation, scavengers, and nutrient dynamics. We present ideas on how to test the strength and community-level effects of guanaco–puma interactions. We end by discussing how the live shearing of guanacos and other economic activities like ecotourism could benefit from ecologically functional populations of these two iconic species.

5.1.2 *Patagonia, an Ecologically Eroded Scenario*

The Patagonian steppe of Argentina extends from the foothills of the Andes range to the coasts of the Atlantic Ocean. The region encompasses ~790,000 km² of grasslands and shrublands (Gaitán et al. 2020). Upon European settlement in the 1880s, sheep were introduced, and sheep ranching became the dominant economic activity with sheep numbers peaking at 22 million in the 1950s (Soriano and Movia 1986, Chap. 3). Continuous and widespread overgrazing has resulted in ~94% of the Patagonian steppe showing some level of degradation (Del Valle et al. 1998). Intense sheep grazing has led to soil erosion, reduction of plant cover, decline of palatable grass species, and an increase of invasive species. Simultaneously, it reduced the ability of rangelands to provide essential ecosystem services like forage production and carbon sequestration (Aagesen 2000; Gaitán et al. 2018). Native wildlife species, especially mammalian herbivores and carnivores, have suffered severe population declines in the Patagonian steppe (Novaro and Walker 2005). Guanaco populations, which had remained abundant until historical times (Raedeke 1979), declined rapidly because of unchecked hunting, intensive harvesting of *chulengos* (juveniles <1-year-old), widespread range degradation, and competition with sheep for forage (Baldi et al. 2001, 2004; see Chap. 2). Also, predator control programs, sport hunting, and poisoning have affected some populations of pumas and medium-size carnivores (Novaro and Walker 2005), whereas illegal hunting by ranchers has severely impacted others (Franklin et al. 1999). Beginning in the 1980s, a combination of depressed markets and widespread range erosion led to a decrease in sheep numbers along with land abandonment, which in turn benefited puma and guanaco populations reigniting the conflict with remaining sheep ranchers (Novaro and Walker 2005, Chap. 6).

With this renewed conflict, conservationists are advocating strategies that allow for the persistence of wildlife in productive lands. One promising approach involves the use of guanaco populations via live shearing of wild individuals (Baldi et al. 2010; see Chap. 6). However, conservation strategies based on the sustainable use of a single species are often framed within a population level context that overlooks key processes at the community level.

5.2 Guanacos and Pumas: An Enduring Predator–Prey Dyad in Patagonia

5.2.1 *The Makings of a Long-Lasting Interaction*

Fossil and genetic data show that guanaco and puma evolutionary histories are tightly intertwined. Both taxa have Holarctic ancestors (Honey et al. 1998; Johnson et al. 2006) that successfully colonized South America from North America during the Great American Biotic Interchange (Simpson 1950; Webb 1985) ~2.8 million

years ago (Woodburne 2010). The oldest fossils of pumas in South America are from the early-middle Pleistocene of Argentina (1.2–0.8 million years ago; Chimento and Dondas 2018), and recent genomic data suggest that modern pumas even originated in the Neotropics (Saremi et al. 2019). Likewise, guanacos evolved in South America from the lama-like, North American browser *Hemiauchenia* during the late Pliocene, ~two million years ago (Scherer 2013). Pumas and guanacos survived the Pleistocene extinctions, which was particularly severe in Patagonia ~12,000 years ago when the region lost all its megaherbivores (adult body mass > 1000 kg) and most large herbivores and carnivores (>44 kg). Patagonia retained only two ungulate species with adult body masses >70 kg, the guanaco and the huemul deer *Hippocamelus bisulcus*, and one large predator, the puma (Hernández et al. 2019). Whereas huemul deer were apparently restricted to the western forested areas and forest-steppe ecotones, guanacos inhabited mostly the steppe where widespread megafaunal collapse likely intensified guanaco–puma interactions. Indeed, paleoecological inference based on typical and maximum prey sizes indicates that during the late Pleistocene in southernmost Patagonia puma diet was dominated by guanacos (Prevosti and Martin 2013). Essentially, for the last ~10,000 years, pumas and guanacos constituted the only predator–prey interaction involving a large predator and its large ungulate prey in the Patagonian steppe, where they could have been central to ecosystem dynamics until European settlement began in the nineteenth century.

5.2.2 Guanaco Predation by Pumas

Diet data from Argentina and Chile show that guanacos are still an important prey for pumas. In the Argentine Patagonia, 70% of the locations investigated had guanacos representing ~50% or more of the total food biomass in puma scats (Table 5.1). Moreover, surveys of guanaco carcasses in different locations of the Argentine Patagonia reported a high incidence of puma predation on guanacos with 51–78% of the carcasses investigated presenting signs of puma predation (Marino 2010; Fernández and Baldi 2014; Bolgeri and Novaro 2015). Interestingly, and despite long-lasting attempts to eradicate guanacos and pumas from agricultural lands, puma predation on guanacos was similar inside and outside protected areas, suggesting that this interaction persists irrespective of land use (Table 5.1); yet, the importance of guanacos as prey for pumas has declined due to human activities that resulted in low guanaco densities in some localized areas of Patagonia (Novaro et al. 2000). The importance of guanacos as a resource to pumas has been further reinforced by several studies in the Argentine (Palacios et al. 2012; Gelin et al. 2017) and Chilean (Iriarte et al. 1991; Elbroch and Wittmer 2013) Patagonia, where guanaco consumption by pumas increased with increasing guanaco abundance.

A long-term study conducted in Torres del Paine National Park, Chilean Patagonia, has provided detailed information on the trophic interactions between guanacos and pumas. During a 10-year period, 33% of 731 guanaco skulls showed

Table 5.1 Summary of major food categories, presented as percentage of biomass, in puma scats reported by studies in protected areas and ranches, where guanacos were present, in Patagonia, Argentina¹⁻³; Bosques Petrificados, Perito Moreno, and Monte Leon national parks⁴⁻⁵; 25 de Marzo and Doraíke ranches

Region/ protection	References	Major food categories				
		Native		Exotic		
		Guanaco	Other native	Domestic ungulates	Wild ungulates	Other exotic
Patagonia/ protected areas	Zanón-Martínez et al. (2012) ¹	58.6	11.8	0	0	29.6
	Zanón-Martínez et al. (2012) ²	23.2	0.4	0	0	76.4
	Zanón-Martínez et al. (2012) ³	36.5	24.7	0	0	38.8
	Fernández and Baldi (2014)	50.7	26	16.7	0	6.6
	Mean (±SD)	42.3 (±15.6)	15.7 (±12.1)	4.2 (±8.4)	0	37.9 (±29.0)
Patagonia/ unprotected areas	Novaro et al. (2000)	0	1.1	8.7	44.9	45.2
	Zanón-Martínez et al. (2012) ⁴	49.8	24.7	0	0	25.5
	Zanón-Martínez et al. (2012) ⁵	68.8	1	0	0	30.2
	Gelin et al. (2017)	79.6	11.7	3.8	0	5
	Gáspero et al. (2019)	50.8	26.4	7	0	15.8
	Llanos and Travaini (2020)	80.3	5.7	13.9	0	0
	Mean (±SD)	54.9 (±30.0)	11.8 (±11.4)	5.9 (±5.4)	7.5 (±18.3)	20.3 (±16.8)

clear evidence of having been killed by pumas with equal numbers of males (49%) and females (51%) preyed upon (Franklin et al. 1999). Relative to their representation in the population, pumas selected against adults, but proportionally killed greater numbers of yearlings (i.e., young 12–24 months old) and especially chulengos, which were preyed upon four times more than adults (Franklin et al. 1999). Puma predation of chulengos was further investigated over a 5-year period during which 409 newborns belonging to five cohorts were hand captured, equipped with motion-sensor transmitters (Franklin and Johnson 1994), and monitored regularly during their first year. Puma predation on chulengos during their first year of life was the leading mortality cause representing 76 to 83% of all causes of chulengo mortality. Mortality was highest during the first 14 days when 23% of all radio-collared chulengos died, with predation by pumas accounting for 79% of those deaths (Sarno and Franklin 1999). Finally, puma food habits were assessed by analysis of 405 puma scats collected year-round over a 6-year period. European hares

(*Lepus europaeus*, 51%) and guanacos (23%) were the most frequent prey items found in puma scats, but in terms of total relative biomass, guanacos contributed 47% vs. 40% for European hares to the diet of pumas.

An ongoing study in Santa Cruz province is providing additional evidence on the consequential interaction between pumas and guanacos. Since 2020, 10 pumas have been monitored through Iridium collars, which allow the identification and subsequent investigation of potential kill sites using a cluster analysis approach (see Smith et al. 2019a). During the first 2 years of monitoring, 2459 potential kill sites were identified and 1215 were investigated. A total of 327 predation events were confirmed on eight prey species including guanacos (76%), lesser rheas (*Rhea pennata*, 11%), feral horses (5%), sheep (3%), European hares (2%), culpeo foxes (*Lycalopex culpaeus*, 1%), chilla foxes (*L. griseus*, 1%), and two unidentified birds (<1%). Preliminary estimates of puma predation rates on guanacos based upon collared pumas ($n = 7$) for which >60% of potential kill sites were investigated yielded a mean predation rate of 3.5 (± 1.0 SD) guanacos/month/puma.

In summary, studies across Patagonia and other regions utilizing direct field examination of guanaco mortalities, puma fecal analyses, guanaco long-term skull collections, radio collaring of pumas and chulengos, and cluster analyses of potential guanaco kill sites have all provided solid empirical evidence for a strong predator–prey relationship between pumas and guanacos.

5.2.3 Guanaco Behavior and Predation Risk

Some studies have evaluated guanaco behavior under supposed varying levels of risk. In areas with high probability of puma occurrence, guanacos formed large family groups (Marino and Baldi 2014; Iranzo et al. 2018) and increased group cohesion by decreasing individual distances within groups (Iranzo et al. 2018). Moreover, guanacos showed the highest levels of group and individual vigilance and the largest group size in habitats featuring rugged terrain (as opposed to flat and open), like canyons and hills, and tall dense vegetation (as opposed to short and sparse), like meadows and shrublands (Marino and Baldi 2008; Cappa et al. 2014; Taraborelli et al. 2014). Such responses have been interpreted as antipredator behaviors because in these habitats guanacos appeared to be most vulnerable to puma predation (Bank et al. 2002; Bolgeri and Novaro 2015).

In Torres del Paine National Park, a migratory population of guanacos was subject to year-round predation from pumas, especially during the birth season and winter (Franklin 1983; Wilson 1984; Ortega and Franklin 1995; Franklin et al. 1999). These guanacos formed large groups, some containing over 170 animals during the winter. The large aggregations were suspected to be partly related to an adaptation to increased winter predation risk and because of 5–7% increased chulengo mortality with each additional centimeter of snow (Sarno and Franklin 1999).

Another suspected response of guanacos to puma predation risk is shown by preliminary data from Parque Nacional Monte León in Argentine Patagonia. Here,

guanacos underwent strong diel habitat shifts. During daytime, they occupied productive grasslands and meadows in risky canyon hillsides and bottoms, but at dusk moved up the canyons to occupy open, flat, and apparently safer habitats (Verta et al. 2020). Similar diel shifts were reported for vicuñas under strong predation by pumas in the central Andes of Argentina. Vicuñas grazed in highly productive, yet risky, habitats during the day but at dusk sought safety on open llanos, where short vegetation and flat terrain hindered puma ambushing (Donadio and Buskirk 2016; Smith et al. 2019b). Comparable diel movements were observed in guanacos in Chile (Franklin pers. obs.) and vicuñas in Peru (Franklin 1974), both interpreted as antipredator strategies.

5.3 Guanacos and Vegetation

Knowledge on guanaco–plant interactions is mostly restricted to descriptions of guanaco diet and forage selection in different contexts. In northwestern Patagonia (Argentina), guanacos showed greater utilization and preference for grasses, particularly *Poa* and *Panicum*, and graminoids like *Oxychloe*, throughout different habitats and seasons, with grasses representing 60–92% of guanaco diets (Puig et al. 1997, 2001, 2011). In northeastern Patagonia (Argentina), varying population densities (12–29 guanacos/km²) had no effects on diet composition, which was dominated by *Poa*, *Panicum*, and *Stipa* grasses (60–70% of the diet) followed by shrubs (30–35%; Rodriguez et al. 2019); grasses even dominated guanaco diet (45%) in spring, when grass consumption was lowest (Baldi et al. 2004). Similarly, in Tierra del Fuego (Argentina and Chile), grasses (*Alopecurus*, *Poa*, and *Festuca*) and graminoids (*Carex*) were the most important forage representing up to 90% of the diet (e.g., Raedeke 1980; Bonino and Pelliza-Sbriller 1991; Fernández Pepi et al. 2014) irrespective of season (Muñoz and Simonetti 2013), and even in forested areas where grasses were less abundant and browsing increased (Arias et al. 2015). Overall, data indicates a strong interaction between guanacos and a few species of grasses and graminoids (Ortega and Franklin 1988). Yet, how guanacos affect populations and communities of these plants remains unknown.

Work on the closely related vicuña, however, provides a hint on how guanaco herbivory, and indirectly puma predation, could affect vegetation. In the central Andes of Argentina, structural and functional attributes of a grass community grazed by vicuñas were evaluated in 6 pairs of 20 × 20 m treatment and control plots. Treatment plots consisted of 1.5-m-high fences that excluded guanacos and vicuñas, the only large herbivores in the area. Guanacos, however, were ten times less abundant than vicuñas and rarely seen during the study; thus, all grazing responses measured were attributed to vicuñas. After 2 years, treatment plots, when compared to controls, resulted in a 2.2 times increase in cover, a 2.6 times increase in height, a 6.6 times increase in biomass, and a 28 times increase in seed production of grasses. These dramatic effects of vicuña herbivory on grasses were observed in open plains, which provided good visibility for vicuñas and little ambush cover

for pumas but faded in habitats featuring physical attributes that facilitated puma ambushing (Donadio and Buskirk 2016). If the effects of guanacos on grasses are mediated by puma predation and resemble those observed for vicuñas, then it could be expected that the guanaco–puma interaction would influence grass communities across the Patagonian landscapes.

5.4 Guanacos and Nutrient Cycling

How guanacos contribute to nutrient cycling and plant growth is mostly unknown. A handful of reports show that guanaco dung piles, where urine is also deposited, favored adjacent plant growth by concentrating otherwise scarce nutrients (Franklin 1975). Henríquez (2004) compared several vegetative and abiotic attributes between guanaco dung piles and control sites in Chile. He found that plant species diversity, richness, and percentage of organic matter were 3, 4, and 385 times, respectively, higher in vegetation associated with dung piles than in control sites. Likewise, phosphorus, potassium, and nitrogen concentrations were 18, 70, and 137 times higher.

Similar observations have been reported for vicuñas. Topsoil depth, plant diversity, and forage production were higher for vegetation associated with vicuña dung piles in Peru (Franklin 1978). This localized effect could be scaled-up to the landscape level. Vicuña dung piles are circular (1–2 m diameter) accumulations of fecal pellets that amass an average of 7 and 29 kg of fecal material/year/dung pile with densities of 4.3 and 6.7 dung piles/ha in feeding and sleeping territories, respectively (Franklin 1978, 1980); in Argentina, estimates of vicuña dung pile densities range from 11 to 16 dung piles/ha (Donadio and Buskirk 2016). Thus, scaled up to the landscape level, up to 448 kg of fecal material/ha can be mobilized through dung piles every year, a significant amount in arid environments.

Indeed, Franklin (1974, 1982) reported that in the Peruvian Altiplano vegetation associated with vicuña dung piles represented 20% of the total surface of the study area and 10% of total forage production. Dung piles might also provide nutrients and organic material for early stages of plant succession, facilitating the expansion of grass species into areas dominated by bare ground (Franklin 1982, 1983; Reider and Schmidt 2021). Although in vicuñas both sexes use dung piles whereas in guanacos primarily males use dung piles while females eliminate randomly or in dung zones, both species present similar patterns of dung pile formation and use (Franklin 1983; Marino 2018). Thus, guanacos are predicted to influence nutrient dynamics and distribution by creating nutrient hotspots and redistributing large amounts of these nutrients across the landscape.

Whereas dung piles represent one pathway through which guanacos might influence nutrient dynamics, ongoing work on vicuñas at San Guillermo National Park in Argentina is revealing a second pathway. Soil beneath carcasses of vicuñas killed by pumas creates higher soil nutrients (i.e., nitrogen) than adjacent control sites. Furthermore, these effects persisted for several years, suggesting that besides creating temporary pulses of nutrients, vicuña carcasses might also have legacy effects

on the distribution of soil nutrients. Interestingly, carcass effects on soil nutrients are muted in the most productive habitat (i.e., densely vegetated meadows as opposed to sparsely vegetated canyons and plains) because of the high availability of moisture and nutrients already present in meadows (Monk et al. 2021).

Although scanty, available data on wild South American camelids suggest that guanacos have the potential to affect the distribution and availability of organic matter and nutrients that subsequently influence plant growth rates and succession. Whether these effects result in part from guanacos responding to puma predation is still unknown, but possible given that habitat selection and movement patterns of vicuñas appeared to be strongly influenced by the risk of encountering pumas (Smith et al. 2019b).

5.5 Guanacos as a Source of Carrion

Guanacos are large mammals with a mean adult body mass of 97 kg (Carmanchahi et al. 2019). Thus, guanacos represent the most important wild source of terrestrial carrion in Patagonia. Pumas kill guanacos and, like other large carnivores, they sometimes abandon their kills leaving edible uneaten biomass that could be exploited by scavengers. For example, in the Chilean Patagonia, at least 12 species of vertebrates scavenged ungulate carcasses killed by pumas. In terms of biomass, pumas were estimated to leave ~2553 kg meat/month over 1100 km² (Elbroch and Wittmer 2012). As the largest obligate scavenger, the Andean Condor (*Vultur gryphus*) appears to benefit the most from these food subsidies, especially in regions where pumas extensively feed on guanacos. In fact, condors scavenged at least 43% and 35% of the carcasses presenting signs of puma predation in central Chile and Argentina, respectively (Elbroch and Wittmer 2012, 2013; Perrig et al. 2016). If a wild condor covers its energetic requirements with ~20 kg meat/month (the amount consumed by captive individuals; AZA Raptor TAG 2010), the biomass left by pumas would represent a critical food resource for condor populations even if they utilized only a small fraction of the carrion available. For example, 40% of the carrion produced monthly by pumas would be sufficient to meet the monthly energetic needs of ~50 condors. The relevance of this source of carrion increases if we consider the home range size of condors. Indeed, the estimate of 2553 kg of meat/month over 1100 km² represents the carrion available in only 7% of the mean home range size of a condor population in Patagonia (Lambertucci et al. 2014).

The importance of guanacos for condors and other avian scavengers becomes most evident from dietary studies. In the central Andes of Argentina, condors and Mountain caracaras (*Phalcoboenus megalopterus*) scavenged guanaco (and vicuña) carcasses whenever these camelids were available. Here, guanacos and vicuñas made up 88% and 73% of the vertebrate prey items found in 183 and 364 condor (Perrig et al. 2016) and caracara pellets (Donadio et al. 2007), respectively. Moreover, isotopic analyses of molted feathers revealed that camelids represented 45–58% of condor assimilated biomass (Perrig et al. 2016). In the Payunia and

Ahuca Mahuida reserves of northwestern Argentine Patagonia, guanacos represented ~75 and 35% of the total prey items found in 152 and 212 pellets, respectively (Perrig et al. 2021). Similarly, in Chile, Andean condors consumed increasing proportions of guanaco at higher latitudes, a pattern explained by increasing abundances of guanacos and pumas (Duclos et al. 2020). Also, guanaco remains occurred in 63% of 155 Crested Caracara (*Caracara plancus*) pellets in Torres del Paine (Engh et al. 1997). Puma predation represented the main mortality cause of guanacos (and vicuñas) in most of these Argentine (Donadio et al. 2012; Bolgeri and Novaro 2015) and Chilean (Franklin et al. 1999) systems. This evidence suggests that the guanaco–puma interaction might be a key mechanism that supports entire communities of scavengers.

5.6 Guanacos, Pumas, and Trophic Cascades

Existing data shows that where guanacos are still abundant, they represent an important prey for pumas. But could pumas trigger a trophic cascade by limiting numbers and altering behaviors of guanacos? Whether puma predation can limit guanaco numbers is unknown because we lack longitudinal studies on the population dynamics of guanaco–puma systems. Indeed, factors driving long-term population trajectories of wild South American camelids have only been assessed for guanacos in Tierra del Fuego (Zubillaga et al. 2018), a puma-free island, and vicuñas in northern Chile, where data on puma predation on vicuñas is missing (Shaw et al. 2012). In Torres del Paine National Park, increasing guanaco numbers correlated with rising puma densities and increased puma predation, which was particularly intense on juveniles (<1 year; Franklin et al. 1999 and references therein). This increasing level of predation was hypothesized to limit the guanaco population, but long-term supporting data is needed.

Behavioral studies, in turn, show that several antipredator behaviors of guanacos correlate with puma hunting mode. Pumas rely on physical cover for hiding and approaching prey before launching an attack (Sunquist and Sunquist 2002). Thus, habitats with tall grasses and shrubs, rocky outcrops, and steep slopes should be high risk for guanacos. Indeed, guanacos seem to perceive varying levels of predation risk and increase their antipredator behaviors, particularly vigilance, in habitats that favor ambushing by pumas. Increased guanaco vigilance in and avoidance of some habitats have the potential to release vegetation from grazing, setting the stage for a trophic cascade (Fig. 5.1).

Furthermore, diel guanaco movements, a suspected antipredator behavior, could result in a net transfer of nutrients from risky and more productive (e.g., grasslands and meadows in canyon hillsides and bottoms) to safe and less productive habitats (e.g., flat open habitats with short vegetation), thus rearranging the distribution of nutrients in the landscape and supporting vegetation in areas with low nutrient availability. Additionally, increased puma predation in certain habitats could result in uneven distribution of guanaco carcasses creating nutrient hotspots that enrich soil

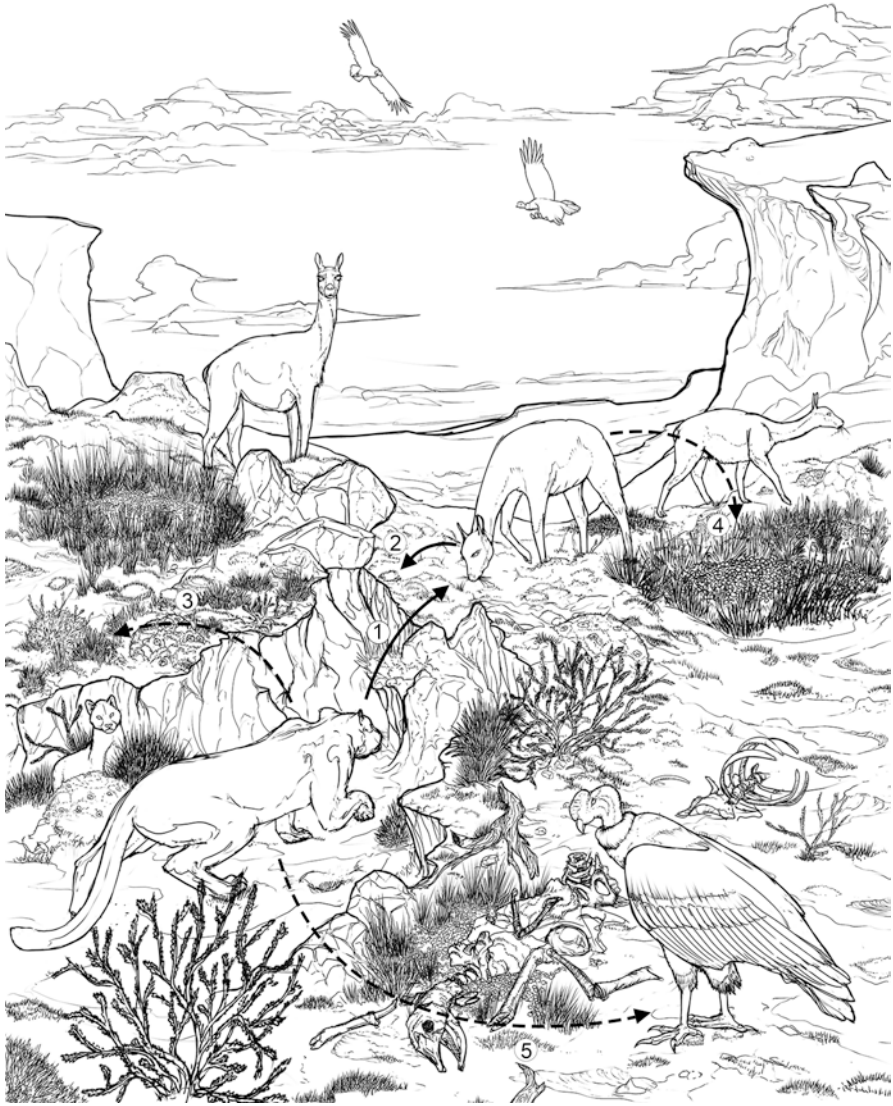


Fig. 5.1 Conceptual model depicting some of the community and ecosystem-level effects of a hypothesized trophic cascade triggered by the guanaco–puma dyad. Solid lines show direct negative interactions. Broken lines show indirect positive interactions. Puma predation on guanacos limits the numbers of guanacos and modifies guanaco behavior (1). Guanaco herbivory suppresses vegetation (2). By affecting guanaco numbers and behaviors, pumas release plants from heavy grazing (3) and influence the spatial distribution of guanaco latrines with subsequent effects on nutrient cycling (4). Killing of guanacos by pumas results in year-round subsidies of carrion for scavengers (5)

pools in these habitats. Also, puma predation might result in a regular and predictable year-round provision of guanaco carcasses for scavengers, especially for those that rely exclusively on carrion as a source of protein for survival and reproduction. We argue that the guanaco–puma interaction triggers a trophic cascade that supports a wide range of species and ecological processes. Current trends of land use across the Argentine Patagonia provide an opportunity to test this hypothesis.

5.7 An Opportunity to Understand Guanaco–Puma Interactions

Rigorously testing predictions derived from the trophic cascade concept is challenging in systems featuring large predators and their ungulate prey (Ford and Goheen 2015; Allen et al. 2017). Key obstacles are the logistical and ethical issues of experimental manipulation, especially of large predators, coupled with replication at the landscape level. Pumas, guanacos, and vegetation represent a simple trophic chain with three fundamental interactions: (1) predators directly and negatively influence herbivores, (2) herbivores directly and negatively affect plants, and (3) predators indirectly benefit plants. These interactions could be quantified individually to evaluate predictions within a trophic cascade framework (Ford and Goheen 2015).

Current trends of land use in the Patagonian steppe have resulted in a mosaic of abandoned and operating sheep ranches plus protected areas. In turn, preliminary data suggest that pumas and guanacos are reclaiming those deserted rangelands. This spatial variation in land use could serve as the basis for a spatially replicated, long-term project directed at evaluating the existence and strength of a trophic cascade triggered by puma predation on guanacos. Basically, this project could take advantage of the varying levels of guanaco and puma abundances observed across locations.

Predicted numerical and behavioral effects of pumas on guanacos could be evaluated through correlations of abundance estimates between pumas and guanacos and anti-predator behaviors of guanacos over time and across sites. Concurrent evaluations of puma predation rates, guanaco demographic attributes, and behavioral budgets would shed light on the numerical and behavioral mechanisms that might be operating. In sites with low puma abundance, this approach should be reinforced with evidence of bottom-up limitation of guanaco numbers. Potential impacts of guanacos on plants can be evaluated through exclosures. Similarly, puma facilitation of vegetation could be tested by comparing relative vegetation differences between exclosures and controls in areas (and habitats) with low and high puma abundances (and activity) and associated risk of predation. Additional aspects regarding enhanced biodiversity, scavenger subsidies, and nutrient dynamics could be tested under this general design.

5.8 Final Remarks

If research confirms that puma predation on guanacos results in widespread ecological effects, then the completeness, complexity, and biodiversity of the extensive ecosystems of arid Patagonia would depend, at least partially, on the interaction between guanacos and pumas. For instance, if pumas keep guanaco numbers relatively low and force guanacos to avoid or underutilize certain habitats, then vegetation would increase in complexity, in turn, fostering and increasing habitat for a host of other Patagonian species ranging from insects to mammals. Similarly, guanaco diel movements forced by predation risk would rearrange nutrient distribution, subsidizing patches of vegetation in less productive habitats providing food and shelter for other organisms. These beneficial effects on vegetation could shield soils against erosion, increase forage production, and promote carbon uptake and storage. Finally, guanaco carcasses resulting from puma predation would likely benefit the scavenger community, including species like the vulnerable Andean Condor, highlighting the far-reaching effects that functional populations of guanacos and pumas could have.

For over a century, pumas and guanacos have been subject to aggressive eradication programs because they conflicted with sheep production. These programs took a heavy toll on both species and their ecological interactions. Currently, conservationist practitioners are proposing economic alternatives to promote the coexistence of humans with guanacos and pumas. These activities might also benefit from the predator–prey interaction involving pumas and guanacos.

Live shearing of wild guanacos could allow ranchers to accept the presence of guanacos on their properties. This approach, however, often focuses on conserving a few populations amenable to management and overlooks the ecological role that the species plays in ecosystems. For example, a managed population of vicuñas near a small community in northwestern Argentina had contrasting low puma predation (Arzamendia and Vilá 2012) when compared to a population located far from human settlements (Donadio et al. 2012). This difference likely arose from pumas being eradicated to protect livestock in communal lands. As a result, the role of the vicuña as prey and carrion subsidy for scavengers (Perrig et al. 2016) was severely compromised. Compared to the vicuña experience, live shearing of guanacos in Patagonia might stand-out by considering and avoiding the problems of eroding the guanaco–puma interaction. For instance, live shearing of guanacos is more likely to be profitable at high guanaco densities (Baldi et al. 2010). Thus, concurrent puma predation could potentially stabilize guanaco populations, modify grazing pressure, and enhance possible and desirable effects on biodiversity and ecological processes.

In the Chilean Patagonia, ranches in the vicinity of Torres del Paine National Park are spearheading puma viewing as a tourist attraction and thus tolerating the presence of pumas in their properties. Sheep losses to pumas are lessened with guard dogs or offset with revenues from activities related to puma and other wildlife viewings (Ohrens et al. 2021; Sarno et al. 2019). Similarly, ecotourism based on native wildlife observation is also emerging in the Argentine Patagonia. These efforts could be bolstered by knowledge of puma and guanaco ecology. For instance,

a deep understanding of guanaco–puma interactions should provide the ecotourism industry with a strong framework for storytelling, significantly improving visitor cognitive experiences of a natural operating Patagonia ecosystem (Hill et al. 2007). Overall, combined sustainable activities of live shearing of guanacos and puma viewing have the potential to conserve, especially outside protected areas, the predator–prey interaction between the guanaco–puma dyad.

Current land use and wildlife recolonization patterns in the Patagonian steppe are allowing the restoration of an ecological mechanism that likely dominated the region for the past 10,000 years. We now have a second chance to comprehend this process and ensure its conservation for the full functioning of Patagonian ecosystems and its benefit to future generations. As scientists and conservationists, we cannot afford to miss this opportunity.

Acknowledgments J. Kantor created the drawing shown in the Fig. S. Buskirk provided major comments that improved the quality of the manuscript.

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