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

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Despite being an underpopulated region, Patagonia has attracted the attention of scientists since the very beginning of its settlement. From classical explorers such as Darwin or D'Orbigny, to modern science including nuclear and satellite developments, several disciplines have focused their efforts on unraveling Patagonia's natural and social history. Today, scientific and technological research is shifting from being shaped by northern agendas, towards more locally oriented objectives, such as the management of natural resources, the modernization of energy production and distribution, and the coexistence of rural and cosmopolitan social lifestyles. At the intersection of all these topics, new conflicts concerning the economy, human development, population, and the proper and long-standing planification and management of the landscape and its natural resources have emerged. These conflicts, of course, have also caught the attention of many interdisciplinary research groups.

This series is aimed at describing and discussing various aspects of this complex reality, but also at bridging the gaps between the scientific community and governments, policymakers, and society in general. The respective volumes will analyze and synthesize our knowledge of Patagonian biodiversity at different scales, from alleles, genes and species, to ecosystems and the biosphere, including its multilevel interactions. As humans cannot be viewed as being separate from biodiversity, the series' volumes will also share anthropological, archaeological, sociological and historical views of humanity, and highlight the wide range of benefits that ecosystems provide to humanity including provisioning, regulating and cultural services.

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Pablo Carmanchahi
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA)
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue
San Martín de los Andes, Neuquén, Argentina

Gabriela Lichtenstein
Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL)
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires (UBA)
Buenos Aires, Argentina

ISSN 2662-3463 ISSN 2662-3471 (electronic)
Natural and Social Sciences of Patagonia
ISBN 978-3-031-06655-9 ISBN 978-3-031-06656-6 (eBook)
https://doi.org/10.1007/978-3-031-06656-6

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

To our families – Silvina, Gustavo, Nicolás, Juliana, Matias, and Julián – and the friendship that grew out of working together, and to all the people that daily contribute to guanaco conservation

Preface

The history of the conservation and use of the guanaco in Patagonia is as old as its first inhabitants. In order to understand the drama of the conservation of this species, it is necessary to weave together zooarchaeological, anthropological, physiological, wildlife management, veterinary, and ecological knowledge. As in other social-ecological systems, neither the ecological system nor the social system can be adequately understood without understanding the linkages between the two, and that they function together (Berkes and Folke 1998). In this book, we propose a holistic multidisciplinary approach to understand the history of the species in Patagonia, as well as to solve the growing complex challenges associated with its conservation and sustainable use.

South American wild camelids in general, and the guanaco in particular, have received relatively little interest in the world's scientific literature. This may be due to its geographical range, which is restricted to the Andean and steppe zones of South America, with a strong population concentration in the Patagonian region. However, in the last three decades, scientific interest in this species has increased, mainly due to the possibility of using some of its populations to obtain fiber and meat, which has opened up a new area of research.

In *Guanacos and People in Patagonia: A Social-ecological Approach to a Relationship of Conflicts and Opportunities*, we have compiled updated information and presented unpublished data on the relationship between one of the most representative species of Patagonian fauna, the guanaco, and human society, and how this relationship has changed over time due to different land uses and productive interests. This book provides information to understand these interactions, in order to contextualize the current situation of this species and, in some cases, to propose possible solutions to conflicts and show ongoing activities aimed at sustainable use and conservation.

The chapters of this book are written for a wide audience, without losing scientific rigor, be it researchers, postgraduate students, policy makers and professionals in conservation and rural development. They are also intended as a tool for enforcement authorities and field technicians on the use and conservation of wildlife, helping to define management actions for this species. Most of the authors are members of IUCN South American Camelid Specialist Group (IUCN – SSC – GECS).

The book is organized into 9 chapters, the first of which provides a taxonomic description of the group and establishes an overview of the conservation status of guanaco populations throughout its range. In addition, the main threats to the conservation of this species in Patagonia are developed in detail, focusing on economic activities linked to livestock farming and oil and mineral extraction.

Chapter 2 provides an introductory and descriptive account of how the native peoples of Patagonia interacted with wildlife, and specifically with the guanaco. This species, of social importance in the indigenous world of the region, was crucial as a source of food and for clothing and shelter. It also shows how the Patagonian landscapes have undergone socio-territorial transformations over the last 200 years that have compromised and modified the domestic modes of reproduction of these human groups and, therefore, also the use of the guanaco. For this reason, both zooarchaeological and socio anthropological perspectives are incorporated in order to achieve a comprehensive understanding of the historical process.

The guanaco has been perceived historically by ranchers as a competitor of cattle for available forage and as a cause of pasture degradation that decreased the receptivity of pastures and thus became a threat to livestock production. Based on these assumptions, on which there is no scientific-technical consensus, management actions were implemented to reduce the number of guanacos on ranches, and more recently, changes in public policies related to guanaco management were promoted. In Chap. 3, these assumptions are tested through a review and synthesis of the evidence (direct and indirect) accumulated to date on the potential for competition between guanacos and cattle for forage resources and the relative impact of each herbivore group on Patagonian grasslands. In addition, aspects related to foraging behavior, diet, and habitat overlap and the relationship of herbivores with vegetation in exclusive and mixed grazing situations are analyzed.

Wildlife health is an increasingly important component of wildlife conservation. With human-induced global change, including loss and degradation of biodiversity and habitat, wildlife is constantly subject to stress factors that expose them to an increasing risk of disease. Chapter 4 provides the first systematic review of available information on guanaco health in the Patagonian region. This information is compiled and analyzed in the context of its relevance for conservation and the main threats to the species. In addition, the influence of natural and anthropogenic factors on the presence and variability of pathogens is discussed and their possible impact on guanaco resilience, management, and sustainable use is analyzed.

Predator-prey interactions involving large predators and their ungulate prey have been postulated to strongly influence ecological patterns and processes in communities and ecosystems. The intensity of these effects appears to be greater in arid environments with simple food webs. Pumas (*Puma concolor*) and guanacos have coexisted in South America for at least 1 million years. However, little is known about how they interact and whether the effects of this interaction carry over to other trophic levels. Chapter 5 reviews and synthesizes data on puma-guanaco interactions, as well as other key aspects of guanaco ecology. This information is then framed within food web theory to argue that puma predation on guanaco can trigger a trophic cascade with possible direct and indirect effects on vegetation, mesopredators, scavengers, and nutrient dynamics. Finally, a research program that could be implemented to test these theories on the influence of puma-guanaco interaction on communities and ecosystems is described. It is concluded that critical ecological mechanisms, such as predator-prey interactions involving large mammalian predators and their ungulate prey, will be conserved only if these mechanisms are explicitly recognized.

In southern Patagonian Argentina, the conflict between guanaco conservation and sheep farming has increased in recent years due to stochastic and socioeconomic factors. Chapter 6 analyzes the changes in international and national public policies related to guanaco conservation and management in Argentina and their relationship with the growing conflict between the sheep farming sector and the guanaco. It presents the complex map of actors involved in regulating the use of wild guanacos, the main milestones in this process, and the most important drivers that influenced the development of public policies associated with the use and conservation of the species. In addition, international policies regarding guanacos are compared with those for vicuñas (*Vicugna vicugna*) and recommendations are made to improve the current situation.

The guanaco was recognized by FAO as a key species for rural development in Latin America, due to its economic value, the demand for its products, and the potential to generate jobs. The use of this wild camelid, considered an herbivore with low environmental impact, has the potential to play a fundamental role in halting desertification processes in arid Patagonian ecosystems and to provide an economic alternative for local producers. Chapter 7 summarizes the results of the research that served as the scientific basis for the elaboration of provincial and national regulations governing guanaco management in Argentina. Given the different possibilities of use established in the National Management Plan for this species, the economic contexts for the use of guanacos in the wild and in captivity are analyzed and compared. It also presents the challenges that this activity still presents in the commercialization of its products. Finally, it is discussed whether the actions carried out since the elaboration of the National Guanaco Management Plan (2006) to date can be considered to have fulfilled the criteria of adaptive management.

In order to provide a comprehensive overview of the status of wild guanaco populations in the region, Chap. 8 compiles, summarizes, and analyses previously reported information, strengthened with unpublished data, including current studies, which allow a better understanding of the historical and current context of this species in Chilean Patagonia. This information is complemented with biological and ecological data ranging from social structure and behavior to population dynamics and genetics.

Finally, Chap. 9 summarizes some of the findings with policy impact mentioned along the book and draws lessons and opportunities for the conservation and sustainable use of the guanacos in Patagonia.

The topics covered in this book are developed by researchers with extensive experience in zooarchaeological, ecological, physiological, and ethological studies, as well as in the management and conservation of this emblematic species of the Patagonian arid environments.

We thank the National Scientific and Technical Research Council (CONICET) for financial and institutional support. Each chapter of the book has been peer reviewed by at least one reviewer and the editors. We thank the reviewers that took the time to provide helpful feedback (all in alphabetical order): Larry Andrade, Fikret Berkes, Steven Buskirk, María Laura Guichón, Laura Estefanía, Warren Johnson, Gisela Marcoppido, Carl Mundt, Morty Ortega, Diego Rindel, Mauricio Soto Gamboa, Alma Tozzini, Bibiana Vila, and Mike Wisdom.

It is almost impossible to work on guanacos and not feel passionate about them. We hope to inspire you with our enthusiasm and that of the authors.

San Martin de los Andes, Argentina — Pablo Carmanchahi
Buenos Aires, Argentina — Gabriela Lichtenstein
March 28, 2022

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Chapter 1
Taxonomy, Distribution, and Conservation Status of Wild Guanaco Populations

Pablo Carmanchahi, Martín Cristian Funes, Antonella Panebianco, Pablo Francisco Gregorio, Leonardo Leggieri, Antonela Marozzi, and Ramiro Ovejero

1.1 Taxonomy and Phylogeny

Long before the birth of Carl Nilsson Linnæus, indigenous groups called the guanaco in different ways. For instance, the people of Tierra del Fuego archipelago called the guanacos "amere" (Yámana) and "yoohn" (Selknama), while people from continental Patagonia called them "luan" (Mapudungun) and "nau" (Tehuelche).

P. Carmanchahi (✉)
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina
e-mail: pablocarman@comahue-conicet.gob.ar

M. C. Funes
IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina

Wildlife Conservation Society Argentina, San Martín de los Andes, Neuquén, Argentina
e-mail: mFunes@wcs.org

A. Panebianco · P. F. Gregorio · L. Leggieri · A. Marozzi
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina
e-mail: apanebianco@comahue-conicet.gob.ar; pablogregorio@comahue-conicet.gob.ar; antomarozzi@comahue-conicet.gob.ar

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_1

The specific epithet guanicoe and the name "guanaco" come from Quechua, a language far extended over Andean pre-Hispanic people related to the Inca Empire. In Quechua, this species was called "wanaku," corresponding to the phonetic equivalent to "guanaco." The Quechua language was, at that time, the dialect necessary to trade between people. Since the beginning of trade in guanaco skins and meat (see Chap. 2), the Quechua name "wanaku" has spread widely. Indeed, this is the word that reached Müller's ears when he first named the guanaco *Camelus guanicoe* in 1776.

About the phylogeny of *Lama guanicoe,* modern camels or South American camelids belong to the order of Artiodactyla (Owen 1848), suborder Tylopoda (Illiger 1811), and the family Camelidae (Gray 1821). The Camelidae appeared during the middle Eocene in North America (Honey et al. 1998; Fig. 1.1). The earliest known ancestor of the camelid family is Protylopus, a 30-cm tall animal (Stanley et al. 1994) that inhabited the North American savannas during the Eocene (~45 Mya, millions of years ago). *Poebrotherium wilsoni*, another of the earliest members of the family Camelidae, is recorded from the late Eocene through the early Oligocene. During the next million years, speciation and extinction processes of at least two tens of camelid genera were recorded (Honey et al. 1998; Rybczynski et al. 2013).

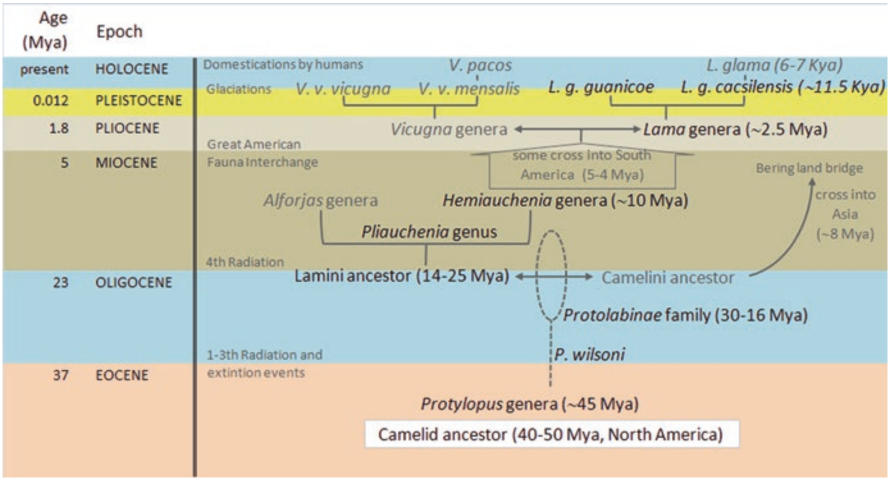

Fig. 1.1 Scheme of the divergence of camelids from a common ancestor 40 to 50 million years ago (Mya), focused on *Lama guanicoe* evolution. Kya: thousands years ago

R. Ovejero
IUCN SSC South American Camelid Specialist Group (GECS),
San Martín de los Andes, Neuquén, Argentina

Instituto de Ecología Regional (IER), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Tucumán (UNT),
San Miguel de Tucumán, Argentina
e-mail: rovejero@tucuman-conicet.gob.ar

According to Honey et al. (1998), the Camelidae family underwent four radiation events. The first event took place in the late Eocene through the early Oligocene, represented by the camelids *Poebrotherium* and *Paratylopus.* The second radiation took place from the late Oligocene through the early Miocene with the stenomy line radiation (*Blickomylus*, *Rakomylus*). These species became extinct in the middle Miocene (Meachen 2003). The "sub-family" Protolabinae appeared in the third radiation, in the late Oligocene and early Miocene. The "subfamily" Camelinae, which includes the "tribes" Lamini and Camelini, appeared between ~17.5 and 14 Mya, during the fourth radiation. The divergence timing between the Lamini and Camelini is still ambiguous, partly due to systematically problematic taxa, including the genus *Aepycamelus* (Lynch et al. 2020). Honey et al. (1998) attributed *Aepycamelus* (~17.5–6 Mya) to the Lamini, while observing that members of this genus could also be ancestral to both Lamini and Camelini. Contributing to the discussion, studies based on mitochondrial data estimated the divergence of Lamini and Camelini to approximately 25 Mya (Cui et al. 2007). The tribe Lamini includes the New World camels, to which the South American Camelids (SACs) belong, while Camelini includes the Old World camels (Webb 1974; Harrison 1985; Wu et al. 2014).

The generic diversity of camelids decreased during the late Miocene when *Aepycamelus* and the last members of the Protolabinae were recorded (Honey et al. 1998). Now, when did the *Lama* genus originate? From the Pliauchenia genus of Lamini, the *Hemiauchenia* and *Alforjas* genera evolved in the middle Miocene (~10 Mya; Webb 1974). The previous North American camelids disappeared in the late Pleistocene (Kurtén and Anderson 1980). Still before that, during the Pliocene, some of the species of the Hemiauchenia tribe entered and dispersed to South America (Gasparini et al. 2017), giving rise to the members of the actual SACs. In 1758, Linnæus described the two domestic species of the SACs as *Camelus glama* (llama) and *Camelus pacos* (alpaca) and placed them together with the domestic old world camelids *Camelus dromedarius* (dromedary) and *Camelus bactrianus* (camel) in one gender only (Wheeler 1995). The two wild species of SACs, guanaco and vicuña, were later described as *Camelus guanicoe* (Müller 1776) and *Camelus vicugna* (Molina 1782), respectively. In 1800, Cuvier classified SACs in the genus *Lama* (Hemming 1958), and in 1924, vicuña was separated from the other SACs creating the genus *Vicugna* (Wheeler 1995). More recently, molecular data confirmed that the genera *Lama* and *Vicugna* diverged 2.5 million years ago from which two actual wild species derive: *Lama guanicoe* and *Vicugna vicugna*, respectively (Kadwell et al. 2001). Recent genome-scale results for wild and domestic SACs confirm the existence of two subspecies in both wild SAC genera: *L.g. guanicoe* and *L.g. cacsilensis*, and *V.v. vicugna* and *V.v. mensalis* (Fan et al. 2020). Fan et al. (2020) also found that the alpaca was domesticated from *V.v. mensalis*, and the llama was domesticated from *L.g. cacsilensis*. These results confirm the genetic study of Marín et al. (2017). On the other hand, archeozoological evidence (Goñalons 2008) places the vicuña domestication in the wet Puna ecosystem of the central Andes of Peru, 6000–7000 years ago, and the guanaco domestication in the dry Puna of southern Peru, Chile, and Argentina.

Analysis of the guanaco genes and genome showed a demographic expansion 400,000 years BP (Before Present), coinciding with the Mindel-Riss/Holstein interglacial period, and a subsequent substantial guanaco population decline from 200,000 to 10,000 years BP, overlapping with the last two major glacial periods (Marín et al. 2013; Casey et al. 2018; Fan et al. 2020). But how are these global events related to the existence of different *L. guanicoe* subspecies? What is the causal inference of the divergence into two subspecies? Glacial periods appear to have helped the isolation of populations, but the crucial geographic barrier is the rise of the Central Andes Plateau, including the Altiplano and Puna regions, which is 1800 km long and 300–400 km wide (Marín et al. 2013). Paleontological evidence indicates that guanacos have occupied the regions surrounding the altiplano since at least 780,000 years BP (Cajal et al. 2010), and their distribution was influenced by repeated periods of glacial build-up and melting even (as recently as the Last Glacial Maximum near 25,000 years ago) (Hoffstetter 1986; MacQuarrie et al. 2005; Rabassa et al. 2011). Recent phylogeographic studies indicate the existence of two main haplotypes: the Northwest haplotype (*L.g. cacsilensis*) and the Southeast haplotype (*L.g. guanicoe*, Marín et al. 2013). Using microsatellites and mtDNA analyses suggest that a small population of *L.g. cacsilensis* was isolated during glaciations on the east side of the Plateau, originating to *L.g. guanicoe*. This original population showed a recent expansion 11,500 years ago, at the start of the Holocene deglaciation process in southern South America (McCulloch et al. 2000; Marín et al. 2013), while *L.g. cacsilensis* expansion was restricted by the Atacama Desert (Marín et al. 2013). The populations with individuals of both haplotypes heritage or mixed genetic heritage in the contact zone (West of the continent between 20° and 35°S) could be explained by anthropic translocation by Amerindians or early Europeans of individuals from the Andes to the coast (Politis et al. 2011).

Finally, a single major demographic event occurred 400–600 years ago when the guanaco suffered a drastic decline in abundance, genetic diversity, and distribution (Buc and Loponte 2016; Toledo 2010; Loponte and Corriale 2020; Fan et al. 2020). The environmental consequences of the Spanish conquest were the invasion of European domestic herbivores (especially cattle and horses), indiscriminate hunting of native species, and human manipulation of the environment, as pointed out by Darwin's pioneering observations (1839).

1.2 Distribution and Conservation Status

The guanaco has been the most widely distributed Artiodactyl in South America since the end of the Pleistocene (Cabrera 1932; Menegaz et al. 1989). In pre-Hispanic times, guanaco populations occupied a wide variety of habitats from southern Peru using the Andes Mountain Range as a bridge to settle in Argentine Territory from the north to its southern limit in Tierra del Fuego and Navarino Island (Cunazza et al. 1995; Wheeler 1995, 2012; Carmanchahi et al. 2019; Fig. 1.2). The species was distributed in most of the South American environments: the desert and xeric

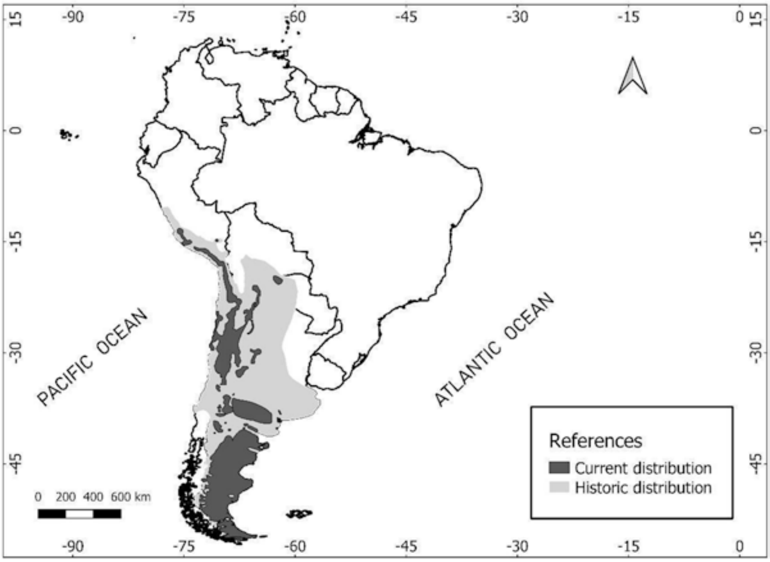

Fig. 1.2 The geographic distribution range of the guanaco (Modified from Franklin et al. 1997, Wheeler 1995), historic distribution (light gray), and current distribution (dark gray)

shrublands; montane grasslands in Peru, Bolivia, Argentina, and Chile; grasslands, shrublands, and savannas located in Bolivia, Paraguay, and Argentina, including the Chaco savanna, Monte Desert, and the Espinal ecoregions; the Temperate Forest; and the Andean Patagonian Steppe (Dinerstein et al. 1995; González et al. 2006; Acebes et al. 2010).

Guanacos inhabit a high diversity of environments, most characterized by a highly seasonal climate with dry winters (Franklin 1983). The guanaco has several physiological and ecological attributes that allowed the species to survive in a variety of environments; some of these adaptations include the presence of plantar pads that provide support in different substrates; the presence of three stomachs that facilitate the assimilation of nutrients; cleft lips that help the vegetation trimming; and molars adapted to vegetation with high lignification (Franklin 1983). Also, there is high variability in the diet and the possibility of changing between different trophic items depending on availability at the local level. For example, in habitats where livestock is present, the guanaco tends to consume more shrubs; in contrast, when livestock is absent, the species increases grass consumption (Raedeke 1979; Baldi et al. 2001).

The guanaco is currently categorized as Least Concern in the IUCN Red List of Threatened Species (Baldi et al., 2016). This categorization is adequate for some areas of guanaco distribution, but not for all of them. The IUCN categorization does not consider the particularities of some populations, especially in the North of South America, where some relictual populations are the last reservoir of the species in that country. In some cases, even bibliographic information is notoriously scarce.

For that reason, here we provide a summary of that information that is not easily available.

As mentioned before, there are two subspecies of guanaco. Peru is one of the few countries where there are records of the *L.g. cacsilensis* subspecies. In this country, the last estimation was recorded in 2009, and a population of 3800 individuals was registered (Linares et al. 2010). Due to its progressive decline and the pressures faced, this species was included in Supreme Decree No. 034-2004-AG in 2004, which categorized it as an endangered wildlife species and prohibited hunting, capture, possession, transport, or export for commercial purposes. In 2014, the list of species was updated (Supreme Decree No. 004-2014-MINAGRI), and the guanaco was reclassified as a "Critically Endangered" (CR) species (Table 1.1). Most guanacos inhabit the Puna region (Linares et al. 2010; Castillo-Doloriert et al. 2016), and the most abundant population in Peru is located in the Calipuy National Reserve. The population is stable, with a slight downward trend, and harbors 418 individuals. Other populations of similar size are in Chavín (456 individuals), and 300 animals were reported in Huallhua, near the Pampa de Galeras' vicuña reserve. Some smaller populations are also recorded in Machahuay, Yanaque, and Vilani, and all have less than 100 individuals (Linares et al. 2010). Currently, there are records of animals using the Lomas Costeras ecosystem in eastern Peru during the dry season (January–April). At least one family group and one solitary juvenile female were identified. Possibly, these individuals moved approximately 30 km from the Santa Lucía region to Lomas de Marcona and the San Fernando National Reserve (Castillo-Doloriert et al. 2016).

In the Bolivian Gran Chaco, there are records of *L.g. guanicoe*. In this country, the guanaco is protected by the Supreme Decree No. 11238 of 1973, prohibiting hunting and capturing of this species (Villalba 1992). The "Red Book of the Vertebrates" categorized the species as "Endangered" due to the reduction and distribution of its populations. It was later reclassified as "Extinct" in the highland populations of Bolivia (Cuéllar Soto and Nuñez, 2009). Recently, the classification was modified and is now categorized as "Critically Endangered" (Table 1.1) because

Table 1.1 Categorization of guanacos according to their conservation status in the countries that include their current distribution

Country	Category	Categorization by zone	Reference
Peru	CR (critically endangered)	The entire country	Decreto Supremo N° 004-2014-MINAGRI
Paraguay	EN (endangered)	The entire country	Saldívar et al. (2017)
Bolivia	CR (critically endangered)	The entire country	Tarifa and Aguirre (2009)
Chile	LC (least concern)	From the Aysén region to the Magallanes region	Decreto Supremo N° 33/2011-MMA
Chile	VU (vulnerable)	From the Arica and Parinacota region to the Los Lagos region	Decreto Supremo N° 33/2011-MMA
Argentina	LC (least concern)	The entire country	Carmanchahi et al. (2019)

there are some individuals (form a relictual and isolated population) and are being threatened by hunting and habitat loss (Cuéllar Soto et al. 2017).

In Paraguay, there is only one confirmed population in the Médanos del Chaco National Park, NW of the country, representing the most extreme northeastern distribution of the species. This population has about 50 individuals and, due to its reduced size, is categorized as "Endangered" (Cartesa et al. 2017; Table 1.1). Due to identifying a narrow link between the Paraguayan and Bolivian populations, recently, both countries signed an agreement to generate common strategies for conserving the species (Cuéllar Soto et al. 2017). In the Gran Chaco, it has been observed that populations have a differential use of space, oriented toward grassland areas. Regrettably, this ecosystem is decreasing due to the process of arborization, becoming the most important threat, even greater than illegal hunting or the competition with domestic livestock (Cuéllar Soto et al. 2020). Also, the observation of solitary individuals is notorious, possibly sub-adults that do not integrate new social units due to the low density of animals (Cuéllar Soto et al. 2017).

Chile is the second-highest density country of guanacos after Argentina. The guanacos live in different environments in this country, including dry central Andean Puna, the Atacama Desert, Chilean scrublands, the Valdivian forest, Magallanic forests, and the Patagonian steppe. The populations of northern Chile correspond to *L.g. cacsilensis,* and the southern populations belong to *L.g. guanicoe* (González et al. 2013). In central Argentina and Chile, contact zones between *L.g. cacsilensis* and *L.g. guanicoe* have been identified; these individuals contain inheritances from Southeastern and Northwestern guanacos, so they are considered a hybrid lineage (González et al. 2013; Marín et al. 2013). The conservation status of the guanaco in the country differs throughout its distribution. While in central Chile it is categorized as "Vulnerable," in the extreme south of the country it is categorized as "Least Concern," and these populations are managed in certain areas (Supreme Decree No. 33/2011-MMA; Table 1.1). The estimated population ranges between 270,000 and 290,000 individuals approximately, with a global upward trend, influenced by the southernmost abundances (González and Acebes 2016).

In Argentina, the most abundant populations of guanacos are in Patagonia, especially in Chubut, Santa Cruz, Tierra del Fuego, and South of Mendoza provinces (Fig. 1.3). However, there are several fragmented populations with low or very low densities in some environments of Chubut, Río Negro, and Neuquén (5 to 2 guanacos/km^2) (Cunazza et al. 1995; Puig et al. 1997, 2003; Baldi et al. 2001; Schroeder et al. 2014). Populations with low densities are found in Catamarca, Tucumán, La Rioja, San Juan, and Northern Mendoza provinces. For the rest of Argentina, densities are below 1 guanaco/km^2. Some relictual populations are in La Pampa, Córdoba, and Buenos Aires Provinces (Carmanchahi et al. 2019). The extent of the guanaco's presence and occupation area suggests that the species should be classified as "Least Concern" (Table 1.1). Still, this categorization should be taken with caution since although the population trend in Patagonia during the last decade has been increasing, populations from Puna and peri Puna, Chaco, La Pampa, and Buenos Aires are

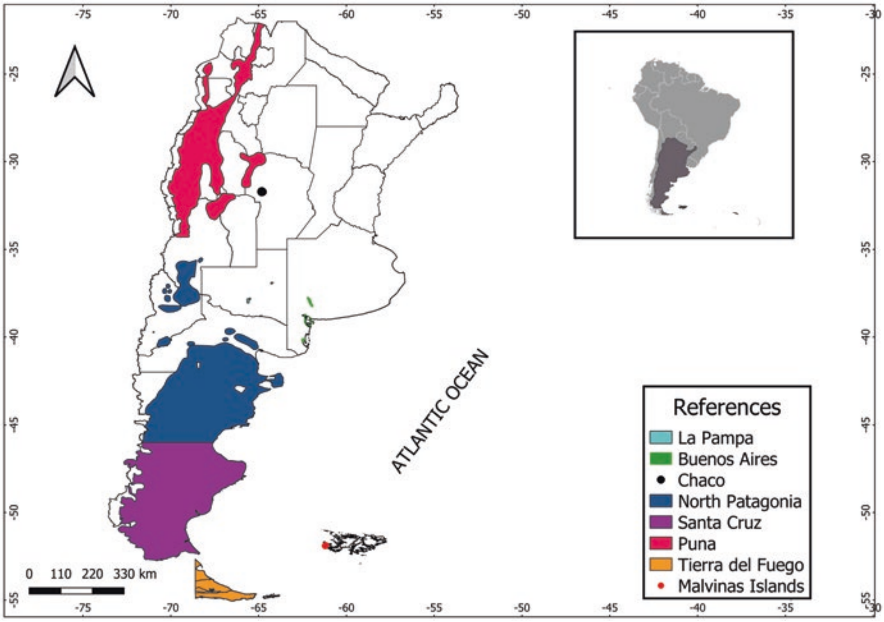

Fig. 1.3 Distribution of *Lama guanicoe* populations in Argentina (Modified from Carmanchahi et al. 2019). The populations of Buenos Aires, La Pampa, Chaco, and Malvinas Islands are relictual, so the polygons representing them are so small that they are not very visible at the scale used in this map. For this reason, the Chaco and Malvinas Islands are represented for a colored point

Table 1.2 Categorization of guanaco populations according to their conservation status in Argentina (Carmanchahi et al. 2019)

Population	Category
Puna and peri-Puna (San Juan, La Rioja, Catamarca, Tucumán, Jujuy, Salta)	EN (endangered)
Chaqueña (North-Central Córdoba)	CR (critically endangered)
Buenos Aires and La Pampa	CR (critically endangered)
Northern-Central Patagonia (Mendoza, Neuquén, Río Negro, Chubut)	LC (least concern)
Southern Patagonia (Santa Cruz)	LC (least concern)
Fueguina (Argentine sector of Isla Grande de Tierra del Fuego)	LC (least concern)

in danger or critical (González and Acebes 2016; Carmanchahi et al. 2019). Therefore, it is crucial to assess the conservation status at the regional or subregional level (Table 1.2).

1.3 Evaluation of Local Populations in Argentina

1.3.1 Puna and Peri-Puna Ecoregion (San Juan, La Rioja, Catamarca, Tucumán, Jujuy, and Salta)

Estimates range between 18,000 and 20,000 individuals in the entire region (approximately 513,165 km^2), mainly in fragmented populations and limited areas (Baigún et al. 2008). Most of the individuals are concentrated in the San Juan (74%), followed by Catamarca (10%) and La Rioja (9%) populations (Baigún et al. 2008). The abundance of the populations in Jujuy, Salta, and Tucumán is low, close to 700 individuals (Baigún et al. 2008); they are restricted to isolated patches and spatially disconnected. The main threat in these areas is poaching.

1.3.2 Chaco Ecoregion (Northern-Central Córdoba)

The distribution of the Chaco population is restricted and isolated from others (Costa and Barri 2018; Geisa et al. 2018). The main threats are poaching and habitat loss due to the introduction of domestic species and agriculture. Population estimates do not exceed 100 individuals, and the extent of occurrence is estimated to be <100 km^2 (Carmanchahi et al. 2019).

As part of a reintroduction project in Quebrada del Condorito National Park (Córdoba province), three experiences of guanaco translocations were carried out, two of them in 2007 and the last one in 2011 (Barri 2016; Aprile 2016). Guanacos were captured from two different sites, the first group was obtained from a wild population of a private ranch in northern Patagonia (40°47′S, 66°45′W) in 2007. Another group of guanacos was translocated from a captive population of a private ranch of Buenos Aires province (38°01′S, 61°40′W) in 2011 (Barri and Cufré 2014). In 2007, traslocations were performed without a pre-adaptation period, and showed a survival rate of 21%, on the contrary, the last one, included a pre-adaptation period between 45 and 60 days, in this case, the survival rate was 96% (Barri and Cufré 2014), 2014. In conclusion, 138 guanacos were released in the area and only 20% of that population survived until 2014 (Aprile 2016), on the other hand, new reinforcements with individuals will be necessary to establish a stable population (Barri 2016).

1.3.3 Buenos Aires and La Pampa Provinces

The population of Buenos Aires is small, and only a few individuals inhabit Monte Tres Picos and Tornquist Provincial Park in the southern part of the province. Information about these populations is scarce and is summarized in Box 1.1.

Box 1.1: One of the Last Guanaco's Population Of Buenos Aires

Alberto L. Scorolli
GEKKO, Grupo de Estudios en Conservación y Manejo,
Universidad Nacional del Sur, Bahía Blanca, Argentina

Guanacos were scarce in the 1940s at Buenos Aires Pampas, and a small-isolated population inhabited the Ventania hills (MacDonagh 1949). In the 1970s, more than 150 guanacos still inhabited Monte Tres Picos and Tornquist Provincial Park, which is the only natural protected area of the grassland hills ecosystem. The nearest population is in the isles of Bahía Blanca estuary at 120 km from the city (Petracci et al. 2021). In the hills, guanaco numbers decreased abruptly due to hunters and poachers' persecution between 1970 and 1984, approaching their extinction. In the 1990s and 2000s, hunting decreased due to rangers' control operations, and the population recovered slowly, reaching 30–50 individuals in 2006 (A. Scorolli, personal observation). Given the risk of extinction due to its small size, governmental authorities supplemented the population with 22 guanacos (October 2007: 2 males and 20 females) born in a captive breeding center of the region. The translocation presented an initial slightly positive growth (Zapperi and Scorolli 2008), but the population remained at the original size after ten years. Some factors that probably prevented population growth were the predation of calves by pumas and forage competition of adults with a very high density of feral horses in the park (Scorolli and Lopez Cazorla 2010). Given that, at present, the guanaco is the only native large herbivore mammal in Tornquist Park, being this population a relict "hilly Pampean" guanacos, demanding more conservation and research efforts.

Moreover, a small population inhabits Bahía Blanca estuary, around 60 or 70 individuals distributed in the Zuritas, Bermejo, and Embudo Islands (Petracci et al. 2021). The main risk seems to be poaching and diseases transmitted by exotic species (feral goats) and livestock. Also, the isolation of the population may be a risk because low connectivity with other populations can reduce genetic variability (Petracci et al. 2021).

In La Pampa province, the population status of guanacos is similar: they are found in low numbers and fragmented, seriously threatened by poaching. There are currently three population nuclei. One of them inhabits Lihue Calel National Park (Alzogaray 2008; Duval 2017), a natural population that never disappeared completely. In contrast, the other two populations from Parque Luro (Duval 2017) and Pichi Mahuida provincial reserves (Susana Kin, personal communication) were established from a reintroduction using animals from other provinces.

1.3.4 Northern-Central Patagonia (Mendoza, Neuquén, Río Negro, and Chubut)

Within the distribution range of this camelid, the population of La Payunia (southern Mendoza) stands out as one of the most abundant in the central area of Argentina (Schroeder et al. 2014). The guanacos in La Payunia change their spatial distribution throughout the year due to their migratory behavior (Bolgeri 2016). In the northern part of the protected area, around 26,000 guanacos are widely distributed during spring-summer. In winter, less than 4000 guanacos remain in the place due to temporary movements to other sectors of the Reserve and surrounding areas in the south (Schroeder et al. 2014; Bolgeri 2016).

There are no population surveys at the provincial level in Neuquén and Río Negro provinces, but at the local level, some farms have surveys, in some cases associated with specific ecological studies and in others, with regulations that oblige producers to present this information to carry out capture and shearing activities of wild guanacos. Neuquén province harbors two important population nuclei, one located in the north of the province, within a protected natural area, the Auca Mahuida Provincial Reserve. Radovani et al. (2014) and Radovani (2016) estimated average densities of 1.1 to 2.6 guanacos/km^2 on the periphery of the protected area, subject to poaching, and 26.0 guanacos/km^2 in sites with poaching restrictions. The second population is located in the southern part of the province. Estimates in different ranches showed a density between 5.2 and 22.9 guanacos/km^2 (Funes et al. 2002, 2003; Carmanchahi and Rey 2004).

In Río Negro province, the distribution and density of the species increase from west to east. On a farm in the province's central region that sheared free-ranging guanacos between 2005 and 2008, population surveys showed densities ranging from 12.5 to 30.2 guanacos/km^2 (Carmanchahi and Funes 2005; Carmanchahi 2006, 2007, 2008).

In Chubut province, 76% of the available routes (7000 km) were sampled in the 2016 breeding season (Pedrana et al. 2019). From these surveys, a total guanaco population of 657,304 individuals (95% CI 457,437 to 944,059 individuals) was estimated, representing a mean density of 2.97 guanacos/km^2. In areas considered marginal habitats for guanaco, the average density was 0.49 guanacos/km^2, while in habitats considered moderate and suitable for the species, densities were 2.74 and 3.93 guanacos/km^2, respectively (Pedrana et al. 2019, Carmanchahi et al. 2019). It is important to mention that the areas with higher guanaco density were those with lower primary productivity, characterized by low NDVI values, low elevation, and far away from oil exploitation and urban areas. This distribution might not indicate a proper habitat preference but rather an indirect response to exogenous factors, like competition with sheep and a response to direct persecution by ranchers or poaching (Pedrana et al. 2019).

1.3.5 Santa Cruz Province

In Santa Cruz province, 8141 km of road surveys (93% of the routes available in the province) were used to estimate density, finding a mean of 4.79 guanacos/km^2, with a coefficient of variation of 20% (Travaini et al. 2015), and increase according to the habitat categories considered (i.e., marginal, moderate, and suitable; Pedrana et al. 2010; Travaini et al. 2007). The mean density was estimated at 1.12 guanacos/km^2 in areas with marginal habitat and at 7.74 guanacos/km^2 in suitable habitats for the species. Therefore, the total guanaco population for Santa Cruz was estimated at 1,066,600 individuals (95% CI 727,800-1,563,200). As in Chubut, densities tend to be higher in areas with low primary productivity (Travaini et al. 2015).

1.3.6 Tierra del Fuego (Argentine Portion of the Isla Grande de Tierra del Fuego)

The current distribution of the species in the region seems to coincide with that described in 1995, in which the greatest concentration of individuals is placed in the center of the island (Forest-Steppe Ecotone Region, Montes et al. 2000). In this area, abundance is estimated to vary between 23,000 and 33,000 individuals, depending on the time of year (nonreproductive and reproductive, respectively), with an average density ranging from 3 to 5 guanacos/km^2 (Flores et al. 2018).

1.3.7 Malvinas Islands

Guanacos did not originally inhabit the Malvinas Islands but were introduced approximately 75 years ago in different archipelago sites. Now, the remaining population is placed in Staats Island (Franklin and Grigione 2005). Recent research evaluated the genetic diversity of this population, and the results indicated a high genetic variation (higher than expected). Nevertheless, malformations were found in some individuals, which might be considered if this population wants to be preserved (Franklin and Grigione 2005; González et al. 2014). Haplotypes from the Staats islands population were compared with other populations, which seem to be related to guanacos at Monte León National Park in Santa Cruz province. Even so, some of the genetic variability might have originated from other neighboring South Patagonian populations, like Torres del Paine and Pali-Ayke (González et al. 2014).

1.4 Conservation Threats

Although guanacos are still numerous and widely distributed in most of their geographic range, their populations have experienced a substantial decline since the 1800s (Baldi et al. 2010). Over-hunting, habitat degradation (livestock overgrazing), and interspecific competition have significantly declined guanacos across their distribution. At present, their occupation is nearly 26% of their original range (calculated by Ceballos and Ehrlich 2002, based upon Franklin 1982). Specifically, their distributional range has decreased by 58% in Argentina, 75% in Chile, and over 90% in Peru, Bolivia, and Paraguay (Cunazza et al. 1995; Ceballos and Ehrlich 2002). Guanaco populations still face severe threats, which are described in this section and will be developed in more detail in other chapters of this book.

1.4.1 Habitat Degradation Due to Overgrazing by Livestock

The introduction of sheep to Patagonia in the late nineteenth century has dramatically changed the landscape. They were first introduced in the 1880s by British immigrants, from the Malvinas Islands (Aagesen 2000), and the north, primarily from the provinces of Buenos Aires and La Pampa (Aagesen 2000; Coronato 2015). During the next few decades, sheep were raised for meat and wool production, and its industry thrived. By 1914, total numbers had increased to around 10 million in Patagonia and 40 million in the whole country (Aagesen 2000; Mueller 2013; Coronato 2015). Some of the best lands in Patagonia were acquired by foreign entrepreneurs, mainly British, where they established large productive units or ranches (locally called "estancias"; Soriano and Paruelo 1990, Chaps. 2 and 5). The relative proportion of sheep in Patagonia continued to grow in comparison to the total number of sheep in Argentina, from around 25% in 1914 to about 70% one hundred years later (Mueller 2013).

The First World War was of great benefit to the sheep industry in Patagonia. The price of wool tripled, and there was also a heavy demand for meat (Grimm 1994). At that time, even the most marginal lands, with sparse forage, were used to raise livestock (Grimm 1994), which required larger areas to support the number of animals. Although prices returned to their former levels when the war ended (Grimm 1994), sheep numbers experienced a sustained increase until 1952, when their numbers peaked at about 22 million in Patagonia (Soriano and Movia 1986). After that, the industry began to experience a steady decline due to several reasons, including the drift toward wool to the detriment of meat (which had started a decade ago) and led to field overloading, the use of synthetic materials, and new productive activities, like fishing and coal (Coronato 2015). More importantly, a substantial reduction in the quantity and quality of forage made it increasingly difficult to maintain the sheep stock at profitable levels since the cost of the initial overloading and the drift toward was starting to become evident (Aagesen 2000; Coronato 2015).

The negative impacts of sheep introduced in the Patagonian landscape have been recorded since the beginning of the twentieth century. A North American geologist, who conducted an extensive survey of northern Patagonia, was one of the first to warn that ranchers did not allow plants to reproduce and regenerate (Willis 1914). Later, several studies estimated the geographical extent of erosion in Patagonia (Auer 1951; Monteith et al. 1970; Movia 1976, 1981; Castro et al. 1980), reporting that the broadest erosion forms are nearly 100 years old and coincide with the arrival of sheep in the region. In addition, overgrazing also produced land degradation and desertification, which are considered the region's main socioecological problems (Soriano and Movia 1986; Coronato 2015). A study from the late twentieth century concluded that 93.6% of the Patagonian region showed some degree of desertification, and a third of it is severely degraded (Del Valle 1998). More recent studies considering a time frame between 1980 and 2010 showed no signs of recovery or a negative trend in desertification advance, even with adaptive management (Oliva et al. 2016). Some of the consequences of land degradation include the widespread occurrence of high shrub density, the replacement of palatable species with unpalatable vegetation, a reduction in plant cover, the invasion of undesirable species, and limited availability of forage (Bisigato and Bertiller 1997; DHV-Swedforest 1998). It has also led to changes in soil structure, compaction, and erosion.

The negative consequences of continuous overgrazing over a century resulted in a decline of sheep husbandry and the abandonment of many farms by their owners because the expenses of the degraded land could no longer support the number of sheep they once did (Baldi et al. 2004, see Chap. 5). The losses were more pronounced in Southern Patagonia, in provinces like Santa Cruz, where more than 300 ranches (out of 1260) were closed in 1991, exceeding 500 in 1997 (Andrade 2002) and reaching 600 in 2014 (Coronato 2015). Ranchers have pointed out this abandonment of ranches as one of the main factors determining the increase in guanaco numbers during the last three decades in Santa Cruz province (A. Manero, personal communication).

1.4.2 Competition with Introduced Herbivores

The massive introduction of livestock has affected guanaco populations in many ways. After the introduction of sheep, guanaco populations declined from around 7 million in the late nineteenth century to approximately 600,000 individuals in the 1980s (Raedeke 1979; Torres 1985). Among other reasons, interspecific competition by resources has been signaled as one of the major causes of this demise (Raedeke 1979). Both species are considered mixed feeders, and their diets include high proportions of grasses and shrubs (Raedeke 1979; Baldi 1999). A growing body of evidence has addressed the interspecific competition between guanacos and livestock and its consequences for guanaco populations (for a detailed review, see Chap. 2) and showed that competition manifests itself in aspects related to foraging behavior, dietary, and habitat overlap. Regarding foraging habits, studies showed that the diets of these species overlap markedly (Baldi et al. 2001; Baldi et al. 2004; Pontigo et al. 2020). At a spatial level, an inverse relationship between sheep and guanaco densities has been reported in many studies, with sheep occupying the most productive areas, whereas guanacos are displaced to marginal habitats (Baldi et al. 2001; Pedrana et al. 2010; Antún and Baldi 2020).

In some regions of Patagonia, guanacos also share their distribution with an introduced ungulate—the red deer (*Cervus elaphus*)—mainly in the forest-steppe ecotone. At the beginning of the twentieth century, red deer were introduced in Argentina and have increased considerably in abundance and distribution, particularly in Northern Patagonia (Staudt 1978; Flueck et al. 2003). Bahamonde et al. (1986) studied the diet of both species in northern Patagonia and showed that some spring diet overlap occurs, particularly for grasses. Besides the potential competition for forage, red deer could also indirectly affect guanaco populations, especially those at low densities, by supplementing puma's food base and supporting its high densities (Novaro and Walker 2005).

1.4.3 Nonsustainable Hunting and Poaching

In Patagonia, the legal hunting of wild guanacos for commercial purposes has been fundamental for many decades of the twentieth century. The guanaco represented an alternative resource to livestock farming for rural settlers through the capture of newborns ("chulengos") and adults (De Lamo 1999) for different purposes (e.g., meat, coats), including trade of the skins of chulengos and adults (see Chap. 1 for a detailed description of guanacos' historical use).

Records of commercial hunting of chulengos go as far back as the beginning of the twentieth century when around 30,000 dead individuals were exported per season, considering Chilean and Argentinean Patagonia (Holmberg 1902). From the 1940s onward, a sustained trade in guanaco hides was maintained in all countries reached by the distribution of the guanaco (Torres 1985), focusing on the export of hides from newborns. According to the first official records in Argentina, in the 1950s and until the mid-1970s, the export of guanaco skins averaged 70,000 individuals per year (García Fernández 1993). During the next few decades, the legal harvest of chulengos pelts grew into a multimillion-dollar industry. From 1972 through 1979, 443,655 guanaco pelts were exported from Argentina (Ojeda and Mares 1982), reaching around 86,000 coats in 1979, accounting for a sum of US$3.6 million (Ojeda and Mares 1982). From 1976 to 1979, 223,610 chulengo pelts, valued at US$5.6 million, were also exported from the country (Mares and Ojeda 1984). Only in Chubut province, more than 118,000 guanaco hunting quotas were granted between 1984 and 1994. The quota for chulengos exceeded the one for adults and ranged between 1500 and 16,000 individuals for the whole province (Ribeiro and Lizurume 1995). Provincial governments granted hunting quotas without accurate knowledge of population abundance or other important parameters such as birth and mortality rates. Instead, the decision was traditionally based on the declaration of "abundance" provided by the owners and managers of the farms. They considered the guanaco as a competitor of sheep for pastures and used to overestimate the guanaco numbers to obtain larger quotas (Baldi et al. 1997).

In 1993, in the absence of policies and regulations to address the declining guanaco populations, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which had listed the species in Appendix II in 1978, recommended the suspension of fiber and pelt exports from Argentina until a sustainable management plan was implemented. National environmental authorities accompanied the decision by establishing guidelines for controlling export, interprovincial transit, and commercialization activities in federal jurisdiction (Baldi et al. 2006; see Chap. 6). In 2006, the first Guanaco National Management Plan (GNMP) was approved, establishing modalities of use only from live animals (Baldi et al. 2006). However, little has changed in practice; landowners kept pressing for hunting permits, and guanacos kept being hunted on almost all private sheep ranches, particularly in Santa Cruz and Chubut provinces. For instance, the Santa Cruz government intended to declare the guanaco a detrimental wildlife species (i.e., a plague) in the province in 2012 because of "its numbers, biological characteristics, and the economic damage and social harm caused" (see Chap. 6 and 7). The complaints from livestock producers alleged the responsibility of guanacos in several road accidents that had the guanaco as the species involved in those incidents. Many members of the scientific community expressed their opposition to these declarations, which were ultimately unsuccessful. However, the predominant negative perception of guanacos from several sectors remained present and influenced other policies later on. The political pressure continued, and in 2019 an update of the GNMP was released, allowing harvesting and commercial hunting in all the provinces. This permit included the sale of fiber obtained from dead animals (SAyDS Res. N° 243/2019), with very little scientific support and lacking actual knowledge of population status and demographics.

In addition to legal hunting, poaching and illegal trade represent a major problem and result in removing an unknown number of animals each year (Puig 1992). As put in the words of Ojeda and Mares (1982), "*legal values represent only the tip of an iceberg*." Poaching is widespread throughout most of the guanaco's range and is particularly important in Patagonia. Poachers commonly come from nearby towns to areas with access or secondary roads from where to shoot, and hunters are authorized by ranch owners interested in reducing the number of guanacos in their fields. The adverse effects of increased hunting can be even more drastic when the expansion of road networks is associated with disturbances such as large-scale hydrocarbon extraction (see below). In Patagonia, one of the main purposes of hunting guanacos is feeding shepherd dogs (Baldi et al. 2006).

The threats related to poaching have recently become more complex due to the combination with other industries such as hydrocarbon extraction. Oil and gas exploration and exploitation exhibit a geographically concentrated but profound indirect effect on guanaco populations due to increased hunting access along oil roads and trails that form an extensive and complex network (Radovani et al. 2014). In northern Patagonia, province of Neuquén, in the area surrounding the Auca

Mahuida Provincial Reserve, mean guanaco densities declined 93–96%, and mean group size decreased from 9.8 to 5.0 guanacos per group at three sites surveyed during 1982–1983 and 2002–2007, as road density increased from 0.14 to 1.84 km/km^2 of habitat (Radovani et al. 2014). These authors point out that the increase in poaching in recent decades, due to greater access and an urban population that has appropriate vehicles (4 × 4 trucks), has probably been the main cause of the marked decline of the guanaco population in this area of Patagonia. The extensive road network not only increases poachers' access but also makes the labor of park rangers and game wardens very difficult to fulfill since poachers always find an escape route from law enforcement officers (S. Goitía, personal communication).

In southern Patagonia (Santa Cruz province), Pedrana et al. (2010) found that guanaco occurrence increased in the less productive and remote areas, far from cities and oil camps, suggesting that guanacos thrive in areas with less human pressure, including poaching. The high density of seismic lines and oil trails could be linked to increased poaching, a threat to wild guanaco populations in southern Santa Cruz. For example, oil and gas industries have had a vigorous development in southwestern Mendoza, southeastern Chubut, northeastern Santa Cruz, south Santa Cruz, and northern Tierra del Fuego (WCS Argentina, unpublished data). This issue affects guanaco populations and other large vertebrates such as Lesser Rhea (*Rhea pennata*) and Patagonian Mara (*Dolichotis patagonum*).

Both poaching and the illegal trade of meat and fiber continue to be a threat for guanaco populations due to minimal control actions by the provincial authorities. A simple search for guanaco meat on the internet delivers several sale options, despite its origin coming from illegal sources. The control and eradication of poaching are essential if a rational system of use of the species is to be implemented. To this end, coordination between the application authorities, the judicial authorities, and the law enforcement agencies is crucial to protect this species, both at the Federal and provincial levels.

1.4.4 Barriers to Guanaco Movement

Fencing is one of the most ubiquitous linear infrastructures but lacks research about its impact on wildlife populations worldwide, resulting in limited empirical data regarding their effects. Fences are spatially extensive, creating vertical obstacles for wildlife (Jakes et al. 2018). These authors advocate for a greater focus on fence ecology: the empirical investigation of the interactions between fences, wildlife ecosystems, and societal needs. The guanaco is no exception for this lack of information regardless of inhabiting mostly fenced private lands where it shares habitat with sheep and cattle. In Patagonia, we can picture wire fences as one of the most widespread barriers to guanaco movements. They also cause yearlings and adult deaths by entanglement (Baldi et al. 2010; Bank et al. 2002; Raedeke 1979). Ranchers use fences to divide 25 to 100 km^2 areas, with different designs and heights, depending on bovine or ovine management. Man-made barriers and human-related activities have likely been the primary cause of the habitat fragmentation and genetic structure currently observed in guanaco populations in northern Patagonia (Mesas et al. 2021). Similar patterns have been found in Alpine chamois (*Rupicapra rupicapra*; Safner et al. 2019) and red deer (*Cervus elaphus*; Edelhoff et al. 2020). Mesas et al. (2021) describe that private fenced properties could explain the genetic differentiation between guanacos from two very close ranches that, despite their proximity, showed very little evidence of genetic contact.

Regarding demographic effects, in central Patagonia, Rey et al. (2012) explored the impact of two types of fences, estimating an annual guanaco's mortality rate of 1.6% due to fence entanglement, discriminated against in 5.5% annual mortality rate for yearlings and 0.8% in adults. Entanglement of young and adult guanacos was dependent on fence design, being more frequent for adults in bovine fences and yearlings in ovine fences. Although these are unpublished data, it is common to see the separation between guanaco mothers and their newborns (chulengos) that cannot cross the fences when the females initiate a sudden escape movement. In a sheep ranch located in southern Chubut, five of those events were observed during 45 km of linear transects, which could eventually become orphan incidents leading to the death of the newborns (M. Funes, unpublished data).

1.4.5 Impact of Disease

The impact of different diseases on guanaco populations is discussed in Chap. 4, but it is relevant to mention here an emerging threat that has grown in recent years, namely the presence of mange in different areas of the species' distribution. Mange is a disease caused by a mite, *Sarcoptes sp*, which has caused epidemics in a wide range of wild mammal species (Bornstein et al. 2001; Alasaad et al. 2013; Fraser et al. 2016; Escobar et al. 2021). Variable prevalence of sarcoptic mange has been reported in wild camelid populations in Peru, Argentina, Chile, and Bolivia (Castillo-Doloriet 2018). In 2014, an outbreak of mange was detected in San Guillermo National Park, San Juan Province, resulting in a 95% reduction of the guanaco population in 2 years (Ferreyra 2019). Therefore, the study and analysis of mange affecting wild guanaco populations should become an essential component of conservation and sustainable management plans for this species.

1.4.6 Predation by Native and Exotic Carnivores

The main natural predator of the guanaco is the puma (*Puma concolor*, Franklin et al. 1999; Bank et al. 2002). The guanaco has a series of behavioral defensive mechanisms such as detection and alarm calls, cooperative vigilance (Taraborelli et al. 2012), living in groups, and habitat selection, enhancing detection of the predators (Franklin 1982; Bank et al. 2003; Marino and Baldi 2008). Guanaco also possesses a musculature suited to short, high-speed runs (González-Schnake et al. 2000), allowing it to escape from its predator's stalking and surprise attack. As a result of changes in the Patagonian ecosystem, puma populations also declined since they were persecuted for reducing predation on livestock. However, in recent decades, the abandonment of fields due to the wool crisis (see Chaps. 6 and 7) allowed pumas to recolonize much of their former range throughout Patagonia (Novaro et al. 2000; Novaro and Walker 2005). Pumas predate guanacos at high rates where they are abundant (Franklin et al. 1999; Bank et al. 2002), but where guanacos are rare, pumas mainly prey on introduced wildlife (like hares, rabbits, deer, or wild boar), and guanacos are consumed only occasionally (Novaro et al. 2000). However, puma predation may have significant demographic consequences for guanacos, preventing or slowing the recovery of some low-density populations (Sarno et al. 1999; Bank et al. 2002; Novaro and Walker 2005). The impact of predators on their prey depends on the predators' total response to changes in prey density, which is the product of their functional and numerical responses (Messier 1994). Novaro and Walker (2005) showed that the relationship between consumption of guanacos by pumas and guanaco density might be prey-density dependent with a threshold of about 8 guanacos/km^2. Thus, in populations with densities below this level, puma predation may play a significant role in preventing growth in guanaco numbers.

Throughout the guanaco's range in Patagonia, there is variation in population densities, with higher densities in Southern Patagonia than in the Northern part (see Sect. 1.3; Carmanchahi et al. 2019). However, most populations have densities below the potential threshold level for puma regulation (or limitation) proposed by Novaro and Walker (2005). Therefore, under current conditions, puma predation may represent a threat to guanaco populations. Sadly, the scenario in Patagonia is not the result of natural evolutionary processes, but rather the consequence of a series of human-induced actions over the twentieth century related to livestock and wild exotic species introduction (e.g., *Cervus elaphus*), poaching, and hunting.

Predation of guanacos by exotic predators like feral dogs (*Canis familiaris*) is another increasing threat in Patagonia (Zamora-Nasca et al. 2021). The feral dog obtains its resources and breeds independently of humans (Green and Gipson 1994), and in this state, dogs hunt in packs using a cursorial strategy (Farías et al. 2010; Ritchie et al. 2014). They frequently kill animals but do not feed themselves, which is known as surplus killing (Kruuk 1972). The reasons for this behavior are still unknown, although they could be related to learning and development, fun, or simply an innate drive to hunt. All these features provide feral dogs with a very high capacity for damage at a population level. Guanacos are particularly susceptible to being killed by feral dogs (González 2010; Silva Rochefort and Root-Bernstein 2021). Some authors have suggested that guanaco lacks adaptations to escape cursorial pack hunters (Root-Bernstein and Svenning 2016). However, this matter is currently under review (Silva Rochefort and Root-Bernstein 2021). Unfortunately, this conservation problem is not adequately documented. For instance, in Chile and Argentina, it has been described as a frequent problem in many populations (Vargas et al. 2016; A. Schiavini, personal communication), but there is no study about the possible consequences at the population level. In Argentina, there are no available assessments of the impact of feral dogs on guanacos, but some farmers have reported dog attacks on guanacos, especially newborns (chulengos) and young animals (Schiavini et al. 2015). In any case, further research is urgently needed to evaluate the real impact of feral dogs on guanacos and implement proper management actions. This is of crucial importance if we take into consideration the overall and steady increase of feral dogs in the entire Patagonian region.

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Chapter 2
Anthropological Perspective of the Human–Guanaco (*Lama guanicoe*) Interaction Over the Last 6000 Years in the Piedra Parada Area (Chubut Province, Patagonia, Argentina)

Pablo Marcelo Fernández and Gabriel Stecher

2.1 Introduction

Zooarchaeology explores the cultural relevance and meaning of faunal remains recovered in archeological contexts (Reitz and Wing 1998). The human use and attitude toward animals along time is one of the zooarchaeology central topics of interest, but it can also contribute to addressing issues of biological importance, as wildlife management and conservation biology (Lyman and Cannon 2004; Lyman 2006; Braje and Rick 2011; Wolverton and Lyman 2012). The long-term trends in species distribution, changes in habitat, and the role of human populations in relation to these attributes can be provided by the zooarcheological record bringing out patterns that cover timescales beyond the reach of ecological studies (Kay and Simmons 2002; Lyman and Cannon 2004; Frazier 2007, 2010; Rick and Erlandson 2008; Braje and Rick 2011; Wolverton and Lyman 2012; Schollmeyer and MacDonald 2020). In Argentina, zooarcheologists have studied the impact of human populations on regional fauna (Cruz et al. 2015; Abbona et al. 2021), the distribution of species (Cruz 2001; Zangrando and Martinoli 2011; Medina and Merino 2012; Scartascini and Volpedo 2013; Fernández et al. 2015), characterized prey habitat and feeding behavior (Kochi et al. 2020; Tessone et al. 2020), and their

P. M. Fernández (✉)
Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires (UBA), Buenos Aires, Argentina

G. Stecher
Asentamiento Universitario San Martín de los Andes, Universidad Nacional del Comahue, San Martín de los Andes, Neuquén, Argentina

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_2

morphological changes through time (L'Heureux 2008), including domestication (Yacobaccio and Vilá 2016).

Among the animals recovered in archeological contexts, camelids have the greatest potential for reconstructing aspects of their ecological history. Since the 1980s, the study of hundreds of archeological sites has generated an enormous amount of data, in line with the importance of camelids for hunters-gatherers, pastoralists, and farmers, all along the Andes and across the Pampas and the Central Highlands of Argentina (Mengoni Goñalons 2010). Recently, these data were used to inquire about the human–guanaco interactions from a coevolutionary perspective, exploring the effect of hunting pressure on guanaco size (L'Heureux 2008), the changes in the human diet, and the evolutionary and demographic history of this camelid (Moscardi et al. 2020), and the availability of guanaco as a prey through time and the environmental or bioclimatic conditions (Rindel et al. 2021). However, guanaco zooarcheological data have had little impact on the literature on the conservation and management of the species. Mengoni Goñalons´ chapter on the socioeconomic importance of the guanaco in pre-Columbian times, in the volume on the guanaco management (Mengoni Goñalons 1995), is one of the few exceptions. In management plan proposals, the historical use of the species covers one paragraph (Baldi et al. 2006) or simply one sentence (Secretaría de Gobierno de Ambiente y Desarrollo Sustentable 2019).

This perspective overlooks the potential of more than four decades of zooarcheological research. Moreover, it does not consider that the relationship between humans and guanacos is dynamic and strongly linked to demographics, land use, and people's attitudes toward this ungulate through time, as observed in the present chapter. Thus, in this chapter, we review six thousand years of human–guanaco interactions in the Piedra Parada area (Chubut). We will provide archeological and anthropological data that allow us to recreate the demography, land use, and attitudes of people toward the guanaco and show how changes in these factors determined the interaction of humans with these ungulates during this period. The information can be used to understand the state of the current guanaco populations in the area from a long-term perspective. Even, it can stimulate their study since they have not yet been investigated from a biological point of view.

2.2 Human–Guanaco Interactions in Patagonia: A General View

In Patagonia, the guanaco was the most important prey for the ancient human populations of the inland before and after megafaunal extinctions (Mengoni Goñalons and Silveira 1976; Miotti and Salemme 1999; Mengoni Goñalons 1999; De Nigris 2004; Cordero 2012; Rindel 2017). This camelid became a crucial source of food and raw materials for making tools, clothing, and shelter, particularly in the Patagonian steppe (Prieto 1997; Mengoni Goñalons 1999; Caviglia 2002; De Nigris

2004; Santiago and Salemme 2010; Scheinsohn 2010; Sierpe 2020, among others). The dominance of guanaco in the diet exhibits some variation, related to its availability as a prey and the presence of alternative faunal resources. At the interior of the continental forest, subsistence was based on huemul (*Hippocamelus bisulcus*), probably due to the absence of guanaco (Fernández et al. 2016). On the marine coast, the existence of pinnipeds, birds, and fish relativized the weight on the diet of this ungulate (Orquera and Piana 1993; Gómez Otero 2007; Favier Dubois et al. 2009). Nevertheless, humans and guanacos were strongly related, both populations increased rapidly after the Early Holocene, and changes in the human diet are correlated with changes in guanaco populations, suggesting the existence of an ecological link of predator–prey type (Moscardi et al. 2020).

The guanaco social relevance is also reflected in rock art. In the Pinturas River basin and the Central Plateau of Santa Cruz, representations of guanacos are more than 9000 years old (Podestá et al. 2005). The painted hunting scenes of the Cueva de las Manos stand out, with very naturalistic representations of guanacos. The animals are shown followed and surrounded by their hunters, and the hunting tactics can be inferred. The paintings depict group and single hunting with snares, *bolas*, and spear weapons (Aschero 2018). In a second moment, around 7000 years BP, in the Pinturas River area, dynamic hunting scenes were replaced by groups of guanacos in different attitudes as grazing, with their offspring or even giving birth (Gradin et al. 1979). In more recent times, iconic representations of guanacos were less frequent and were now represented by their footprints (Podestá et al. 2005). The figure of the guanaco is still present in the last expressions of rock art, characterized by geometric and abstract motifs. There is even a case of a painting of a guanaco transformed into a horse, with the addition of hoofs and a tail, suggesting that guanaco's iconic value persisted until historical times (Podestá et al. 2005).

The arrival of the Europeans triggered major changes in native societies and their interaction with the guanacos. The first contact with Patagonia and its inhabitants dates to 1520 (Pigafetta 1874 [1536]), but the European influence in these territories was gradual and heterogeneous. The populations and territories closest to the European settlements were the most rapidly and drastically transformed. The interior remained a *terra incognita* for centuries, although the Spaniards tried on several occasions to explore and establish communication routes that would provide access to this territory. At the end of the eighteenth century, the Spanish Crown planned a defensive strategy for its territories in southern Patagonia by founding settlements on the coast (Senatore 2007). Although most of them did not prosper, those that survived became nodes in which interethnic relations between hunter-gatherers and Europeans were established (Nacuzzi 1998). Likewise, they also functioned as a point of introduction of livestock (Berwyn 2001), a source of important socioeconomic transformations for the groups of North Patagonia and the Pampean region (Bandieri 2012).

The introduction of the horse modified many aspects of social organization, such as the frequency and distance of camp movements, and transformed the hunting techniques. The convergence between the adoption of the horse and the gradual increase of exchange points stimulated the development of trade in rhea feathers and guanaco hide. The painted cloaks or *quillangos* were made from the skins of animals about to be born or newly born, hunted by communal parties in which horsemen played a preponderant role. The hides were worked by women, tanned, cut, and sewn to form a cloak, and painted on the inside with geometric motifs of various colors, like those depicted in cave paintings or portable art (Prieto 1997; Caviglia 2002). The cloaks were exchanged in places such as Punta Arenas or Carmen de Patagones and were a prized part of the economy of the aboriginal groups (Prieto 1997). The demand for calf skins (chulengos) increased the predatory impact on this age group and, possibly, on the recruitment capacity of some guanaco populations.

2.2.1 Old Relationship Under New Rules

The emergence of the Argentina and Chile National States brought profound changes in the socio-territorial relations, especially with the native peoples. In Argentina, a political view of the so-called "Indian problem" emerged. Native groups were seen as an impediment to achieving a homogeneous national identity, delaying the consolidation of the frontiers between the new states. In this view, the indigenous groups were an obstacle to the productive economic model that demanded the expansion over the territories they occupied, which was ironically called Desert. The imaginary of "Desert" to a land inhabited by just a few barbarian hunters-gatherers lacking a sense of belonging to the new nation. The Argentine State followed the concept of *Terra Nullis*: "(…) territories are 'discovered' by States when there is no other State [nation] claiming sovereignty over them (…)" not giving the right of possession to the previous settlement of the indigenous peoples (Radovich 2003).

These "empty" lands were necessary for the development of the agricultural-based export model. The internal frontier had become the main impediment to the expansion of sectors commercially and financially linked to the main economic powers of the time, in particular England (Bandieri 1993). Thus, in the last third of the nineteenth century, both Chile and Argentina carried out military actions euphemistically called "Pacification of the Araucanía" in Chile and "Conquest of the Desert" in Argentina. This genocide and ethnocide carried out over the native peoples of Patagonia resulted in the domination of the indigenous groups, and its effects and consequences are still felt today (Delrío et al. 2010). In Argentina, according to official records, between August 1878 and May 1879, 1300 natives (mainly men) died in combat. Another 13,000 people, including women and children, were relocated and forcibly transferred to Buenos Aires. They were then distributed as serfdom or semi-slave labor and were sent to different *estancias*, vineyards, or sugar mills in Mendoza and Tucumán provinces (Mases 2002). A few leaders and their communities, who had prior recognition by the state, were allowed to settle on marginal production lands (Pérez 2011).

The control of the territories by the state led to the imposition of a new logic on land use. First, land sales became a resource to finance the military campaigns, and for this purpose, the *Ley de Empréstito* N° 947 was enacted in 1878. Then, in 1885, the *Ley de Premios Militares* N° 1628 was passed to compensate the soldiers who participated in the Conquest. Both favored the privatization of the territory and the concentration of land in a few hands (Blanco 2012). In 1884, Law 1532 on the "Organization of National Territories" created the *Gobernación* of Patagonia, comprising four jurisdictions whose boundaries correspond to the current provinces of Neuquén, Río Negro, Chubut, and Santa Cruz (Blanco 2012). In the words of Galafassi and Barrios García (2020), the occupation of Patagonia can be associated with the merchant capitalism that is born with modernity itself and imposes the logic of capital on land and human lives. Under the new logic for land use, the guanaco was perceived as a harmful animal, even a pest.

In sum, the human–guanaco interaction has extended over millennia, possibly as part of a co-evolution process. The guanaco, key to the subsistence of most Patagonian societies, also played a relevant role in the symbolism of different groups. Demographic growth and the progressive occupation of spaces increased human disturbance, especially in the last 2000 years. Since the Europeans' arrival and the adoption of the horse, the hunter-gatherers gradually increased the pressure on the guanaco. But the extermination and forced displacement of the indigenous population caused the most significant change. A new mode of production based on the extensive livestock of millions of sheep was implemented, which transformed the guanaco into a pernicious species of little economic and social value. However, the human–guanaco interaction varied in time and space, hence the importance of recreating this relationship at the local level. To highlight this point, we will use the case of the Piedra Parada valley, where both species interacted over several millennia.

2.3 The Piedra Parada Area (North Central Chubut)

The Piedra Parada area is located on the Chubut River middle basin (42° 20′-43° S/69° 30′-73° 30´ W). It comprises a narrow (3 km maximum wide, 400 m a. s. l.) river valley located between Sierra de Huancache and Sierra Negra Mountain ranges, connected with these higher sectors (800–1300 m a. s. l.) through canyons (Fig. 2.1). The aridity (138 mm annual precipitations) and the temperatures ranging between 17 ° C in January and 3 ° C in July lead to the development of the shrub-steppe, but there are very important areas of wetlands (locally known as *mallines*) near the river, as well as shallow lakes and wetlands composed of dense Gramineae grasslands in the highest areas (Aschero et al. 1983; León et al. 1998).

In the area, the oldest human occupations date back to 6000–5300 calibrated years [Cal] before present [BP] (Bellelli and Guráieb 2019). Remains left by hunter-gatherer groups were identified mainly at the Campo Moncada 2 (CM2) archeological site and show the exploitation of animals, plants, rocks, and mineral resources

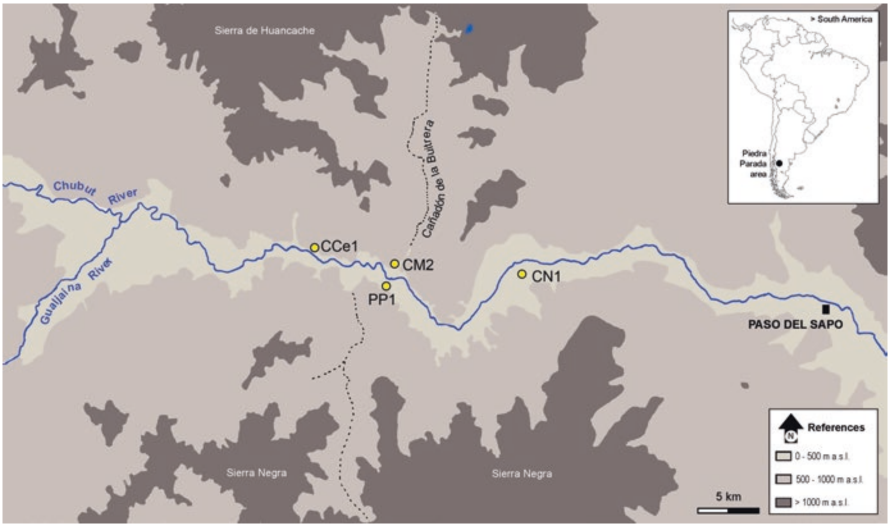

Fig. 2.1 Piedra Parada area, Northwestern Chubut with archeological sites mentioned in this chapter. CCe1, Campo Cerda 1; CM2, Campo Moncada 2; PP1, Piedra Parada 1; CN1, Campo Nassif 1

available in the valley and nearby sectors (Pérez de Micou et al. 1992; Bellelli 2005). The guanaco played a central role in the subsistence of these groups. It was hunted in the vicinity of the rockshelter, transported whole to the site, and there butchered and consumed (Bellelli 1991). The lithic artifacts of this period are long-sized blades (12–20 cm long), and although no hunting artifacts were recovered, there are scrapers used to work the guanaco skins (Bellelli 1991). Knowledge of the resources available in the area—lithic raw materials, minerals for the treatment of hides, fauna—suggests that this was not the first-time hunter-gatherer groups occupied the area, leaving open the possibility of finding early sites.

This first moment is followed by one-thousand-year hiatus, and then occupations occur almost continuously from 4200 Cal years BP to 270 Cal years BP (Bellelli and Guráieb 2019). Since 2300 Cal years BP, the number and variety of archeological sites began increasing (Bellelli and Guráieb 2019), local rock art variant was developed (Onetto 1990), and raw materials from distant sources are recorded: *Nothofagus* sp. wood, and the *Chusquea culeou* bamboo cane from the forest, 100 km W (Pérez de Micou et al. 1992; Marconetto 2002; Pérez de Micou 2002), and obsidian from the Sacanana quarry, 160 km NE from Piedra Parada, in the Somuncura massif (Bellelli et al. 2006). The guanaco was still the main staple and was complemented by choique (*Rhea pennata*), small birds, and *Lagidium viscacia*, a rodent up to 2.5 kg weight (Fernández 2008). The lithic point from contexts dating the last 3200 Cal years BP belongs to arrows, spears, and handheld weapon types and were probably used to hunt guanacos and choiques (Carballido Calatayud and Fernández 2021). For the last centuries, there have been few precisions about the indigenous use of the area. The latest radiocarbon dates reach, at the extreme of their calibrations, up to the first third of the seventeenth century (Bellelli and Guráieb 2019). However, in these contexts, no materials were recovered that can be assigned to historical times (objects of European manufacture or remains of introduced fauna). Likewise, there are no historical records that provide information about Piedra Parada during this period. The foregoing account shows that, at Piedra Parada, human presence increased over time and concomitantly did the same as the hunting pressure on the guanacos. The animals that lived in the valley were the most affected since the human occupation was concentrated there. However, as we will see in the next section, no evidence was found to suggest overexploitation of the species.

2.3.1 Human–Guanaco Interactions from the Zooarcheological View

Several decades of research have made it possible to reconstruct some aspects of the relationship between past societies and guanacos at Piedra Parada (Bellelli 1991; Fernández 2008, 2010; Marchione and Bellelli 2013; Carballido Calatayud and Fernández 2021). The zooarcheological data is based on the comprehensive study of guanaco remains recovered in six contexts dated between 300 and 3500 years Cal BP, from Campo Cerda 1, Piedra Parada 1, Campo Moncada 2,[1] and Campo Nassif 1 archeological sites (Table 2.1). The analysis comprises the anatomical and taxonomic determination, the quantification of the taxonomic abundance, the class age estimation, and the identification of butchery of guanaco carcasses. The methodology used was explained in detail in previous works (Fernández 2008, 2010), so it will be briefly mentioned here. The anatomical and taxonomic identification of guanaco bones was based on osteology manuals (Pacheco Torres et al. 1986; Sierpe 2015) and comparative skeletal collections housed at the Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL, Buenos Aires, Argentina).

Table 2.1 Chronology of the zooarcheological contexts discussed, based on calibrated dates published by Bellelli and Guráieb (2019)

Site	Analysis unit	Time span (in years calibrated BP)
Campo Nassif 1	CN1	313–559
Campo Cerda 1	CCe1 2–3	495–577
Campo Moncada 2	CM2 0–2b	551–918
Piedra Parada 1	PP1	1087–1296
Campo Cerda 1	CCe1 5	1405–3060
Campo Moncada 2	CM2 2c	1421–3484

[1] The fauna recovered from the oldest levels of the Campo Moncada 2 site is not included because it was analyzed with different criteria in the early 1990s (Bellelli 1991).

We employed the NISP (number of identified specimens) and the MNI (minimum number of individuals) to quantify the species representation (Lyman 1994). The age of individuals was estimated based on epiphyseal fusion (Kaufmann 2009), distinguishing between early (newborns, 0–12 months) and late fused bones (adults to senile, 36–48 months). MNE (minimum number of elements) and MAU (minimum anatomical units, Binford 1984) were used to explore biases in skeletal part profiles, helping to infer preference for a specific animal product (meat, fat, marrow). The butchery evidence (cut and percussion marks) was examined with the naked eye, followed by inspection under a 10 × hand lens. A binocular magnifier up to 16 × was used to resolve doubts about inconspicuous specimens. The location of the cut and percussion marks and their morphology were used to infer patterns of prey acquisition, processing, and consumption (Mengoni Goñalons 1999). The analysis considered the existence of other actors and taphonomic processes that could have created and/or modified the bone assemblages (Lyman 1994). In the case of guanaco skin, hair, and fleece remains, the productive process was studied using the concept of an operative chain (Marchione and Bellelli 2013).

At Piedra Parada, 1190 guanaco bones and teeth were recovered, ranging between 83 and 305 per archeological unit (Fig. 2.2). The minimum number of individuals is 3 or 4 guanacos per context except for PP1 (Fig. 2.3). Based on the bone fusion, newborns (up to 12 months) and adults (over 36–48 months) were identified in all bone assemblages except in CCe1 2–3, with no newborns. This data supports the predation on guanaco family groups. The guanaco skeletal parts in assemblages with NISP >100 (all contexts except CM2 2c) suggest that animals entered relatively complete into the sites and were hunted in the surroundings. The diversity of skeletal parts, the percentage of specimens with butchering marks (from 20% to 59% NISP, median 38%), the relative importance of cut marks, and the high

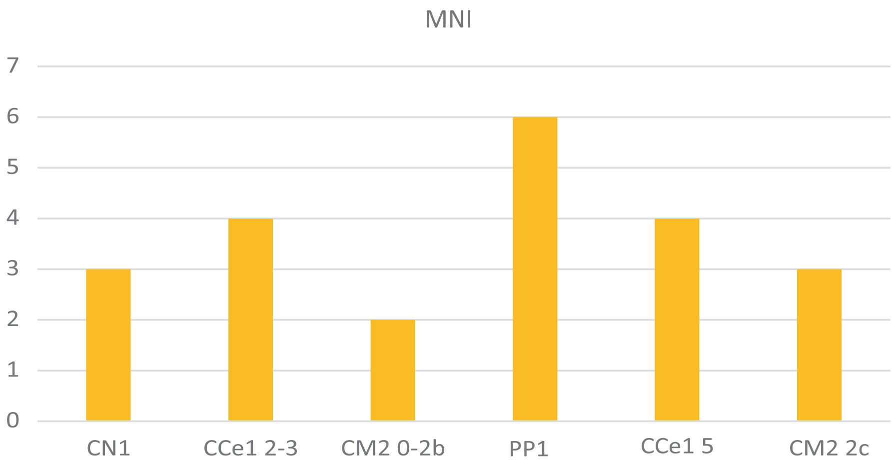

Fig. 2.2 Number of identified specimens of guanaco per archeological contexts of Piedra Parada area. (References in Table 2.1)

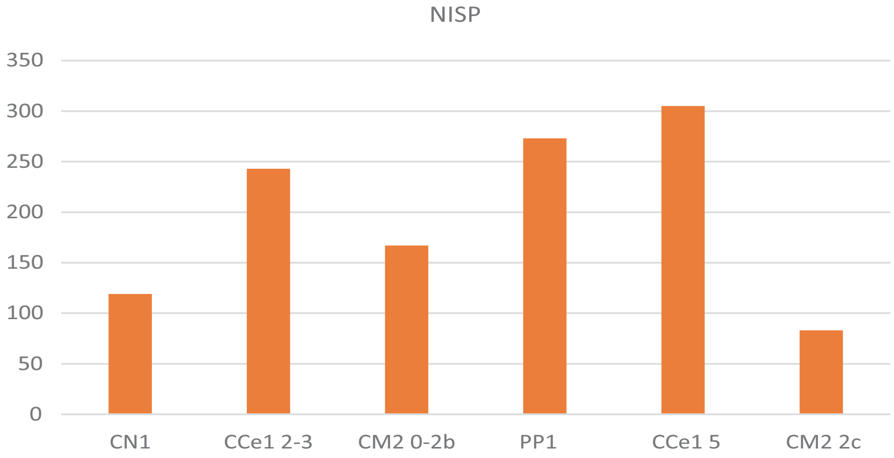

Fig. 2.3 Minimal number of guanaco individuals per archeological contexts of Piedra Parada area. (References in Table 2.1)

amount of intentionally broken bones indicate that the bone assemblages represent the final stage of processing the guanacos' carcasses (Fernández 2008, 2010).

The whole use of the guanaco includes the elaboration of tools with its bones and skin. Guanaco metacarpals or metatarsals were employed to elaborate retouchers and awls. The former was used for lithic tool-knapping and awls to leatherworking. The bones were longitudinally fractured, striking on the proximal end to detach an elongated and thin diaphysis section. Retouchers have a blunt end, and awls have a sharp point (Fig. 2.4). The use of guanaco skins to make manufactured goods was studied at the Campo Moncada 2 archeological site (Marchione and Bellelli 2013). In this site, fragments of leather, rawhide strips, fleece, and fur artifacts were recovered throughout the occupation sequence (Fig. 2.5). There are pieces of guanaco leather, preserved through millennia, that are still flexible and maintain their texture and color. The presence of hair allowed them to assign some of the pieces to guanaco (Marchione and Bellelli 2013). More than 100 fragments have evidence of work, including seams, holes, trimmed edges, scraping marks, twisted cords, and knots that could have been used to bind or sew these garments and artifacts. Some fragments have eyelets, suggesting the making of clothing or bags. In addition, there are fleeces with traces of paint and in the form of swabs, one of them with paint (Marchione and Bellelli 2013).

Recently, hunting techniques at Piedra Parada were reconstructed, combining archeological (lithic and zooarcheological data), ethnographic, and guanaco ecological and behavioral information. On this base, it was proposed the concurrent exploitation of guanacos and choiques (*Rhea pennata*) in the *mallines*, where herbivores' food resources are concentrated. Hunting was focused on territorial guanaco family groups, using an approaching technique: stalking free-moving animals within the effective weapon range (Carballido Calatayud and Fernández 2021).

Fig. 2.4 Guanaco bone artifacts from Campo Cerda 1 archeological site. (**a**) Retoucher [blunt end]; (**b**) awl [sharp point]

2.3.2 Piedra Parada and Northwestern Chubut Under the New Rules

Toward the end of the nineteenth century, the way of life described in the previous section was dislocated. The uninhabited landscape as the result of the military actions at the end of the nineteenth century was reoccupied within the logic of extensive sheep farming (Blanco 2012; Pérez Álvarez 2015). This activity, and its articulation with the British market, is responsible for the first cycle of colonization and internationalization of Patagonia (Coronato 2010). Extensive sheep ranching gave rise to large properties in the sectors with the best productive conditions. The British company the Argentine Southern Land Company Limited (ASLCo) was a representative case of this policy and new socioeconomic relationships. Created in London in 1889, their surface area reached 585,000 hectares, devoted to sheep breeding and wool export to Europe. Leleque, Lepá, and Fofocahuel, localities near

Fig. 2.5 Artifacts and fragments on guanaco hide from Campo Moncada 2 archeological site. Top row (left to right): knot, supple leather, sinew, leather with hair, sewn. Bottom row (left to right): leather with hair and trimmed edges, twisted cords

Piedra Parada, had *estancias* of this company (Míguez 2016 [1985]). As a result of this policy, small and medium-sized landowners and settlers of public lands were relegated to areas with lower ranching value (Blanco 2012).

In the Piedra Parada valley, the first settlers of European origin were mainly Swiss, French, and Spanish, who arrived at the beginning of the twentieth century. Indigenous families from Chile also settled in the valley (Casanueva 2010). In Cushamen and Gualjaina, near Piedra Parada, indigenous families arrived a few years earlier (ca. 1895) coming from Neuquén (Finkelstein 2002; Tozzini 2015). In Cushamen, some people settled on lands granted by the Argentine government to establish an agricultural and pastoral colony that was created in 1902 (Finkelstein 2002). In Gualjaina, an Indian colony was established later, in 1929 (Tozzini 2015). Settlers from other origins and the State itself repeatedly threatened the territorial integrity of these colonies (Finkelstein 2002; Tozzini 2015).

In Piedra Parada, the early settlers were small or medium-sized landowners, whose main activity was low-scale sheep raising, crop farming for self-consumption, and alfalfa fields for animals (Casanueva 2010; Pérez de Micou et al. 2011). An important difference between the valley settlements and the indigenous colonies was that the former occupied different altitudinal sectors (Pérez de Micou et al. 2011) that made livestock production viable. But in the colonies, although some indigenous populations accepted the new lifestyle, they were relegated to productively marginal lands. Thus, they were condemned to enter the labor market as workers in larger establishments with better conditions for livestock production (Finkelstein 2002; Casanueva 2010; Ejarque 2014).

There is very little data on the interaction between these new settlers and the guanacos. In 1911, the ASLCo contracted Indian hunters from the Cushamen Colony to eliminate the guanaco, considering a pest that competed with the sheep for pastures. The result was not as expected, and the contract was not repeated. Instead, the company's laborers were allowed to hunt guanacos as a subsistence supplement and avoid increasing their wages (Minieri 2006: 191). Later, in the 1980–1990s, in interviews conducted during archeological research, some people reported practices linked to the indigenous culture, for example, indigenous spinning techniques and guanaco wool to make some clothes (Casanueva 2010). These practices could suggest a positive valuation of the species. However, there are reports of guanacos hunted during the winter to feed the dogs. Interviews[2] show that the new perception of space and its resources was installed at the beginning of the twentieth century, removed the guanaco from its central place, and relegated it to the position of a competing species with sheep.

2.4 Final Remarks

In this chapter, we show why the history of Patagonian guanacos should be written alongside the history of human societies. Since they entered this region in the late Pleistocene, humans have interacted with guanacos and other camelid species, primarily in a predator–prey relationship. This interaction involved decisions about how to exploit guanacos. Thus, it can be argued that the species has been under human management for over millennia. The bones recovered in archeological contexts support this idea. Also, rock art from some areas of Patagonia shows the guanaco's remarkable role in the symbolic universe of the ancient hunters. The pictures suggest a detailed knowledge of the species and its life cycle, reinforcing the idea of an intimate relationship between humans and this camelid.

For a long time, human populations had low demographics, moving in search of resources, and leaving the area before they decreased. Later, the gradual demographic growth of the human population in Patagonia triggered changes that possibly impacted the guanacos. The most important were the regionalization processes (Martínez et al. 2017), the occupation of previously less frequented spaces such as plateaus or the inner forest (Goñi et al. 2007; Fernández et al. 2013), and the effect of "neighbors" on hunter-gatherer mobility. Together, these factors have increased the pressure on the resources by concentrating populations, limiting access to resources, or incorporating places hitherto undisturbed by humans. European arrival precipitated profound changes that transformed the way of life of human groups in Patagonia long before the national states controlled the region. These changes entailed a new stage in the interaction with the guanaco. Horses modified hunting

[2] The interviews were made in 2009 during the elaboration of the Integral Management Plan for the Piedra Parada Natural Protected Area (Provincial Law 5555/2006) (Bellelli and Fernández 2010).

techniques and prey transport. Historical accounts refer that hunting involved numerous equestrian hunters and the use of fire and dogs. People hunted several types of prey at the same time (Cox 1999 [1863]). Also, hunting in places distant from the camps was made possible using horses (Musters 1871). Moreover, the exchange of *quillangos* led to the overexploitation of some guanaco populations.

This overview is relevant for understanding the interaction with guanacos over time, but it is not enough. Case studies, such as the one presented in this chapter, show the variability in the human–guanaco relationship. We argue that establishing long-term and local-scale interaction trends provides relevant information to understand the current state of a guanaco population. In this sense, at Piedra Parada, there is no evidence of guanaco overhunting or historical occupations related to an increase in the killing of chulengos. It is undeniable that the disarticulation of the indigenous way of life is the turning point in the history of human–guanaco interaction at Piedra Parada (and throughout Patagonia). However, the history before this moment is also important. Assessing the exact value of this information is a task shared by biologists, anthropologists, and archeologists. We trust that the inclusion of this chapter in this volume is a step in that direction.

Acknowledgments The Piedra Parada area has a long research history. Our thanks to the pioneers of the late 1970s and to the archeologists who have continued the work until today. Also, we are grateful for the support and friendship of the people of Piedra Parada. Ana Forlano made Figs. 2.4 and 2.5; many thanks for her work. Dr. Claudio Simeone kindly revised the translation, and his comments and suggestions improved the manuscript. The research was supported by the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, Grant PICT 2017-0525.

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Chapter 3
Interspecific Competition Between Guanacos and Livestock and Their Relative Impact on Patagonian Rangelands: Evidence, Knowledge Gaps, and Future Directions

Natalia M. Schroeder, Victoria Rodríguez, Andrea Marino, Antonella Panebianco, and Fiama Peña

3.1 Introduction

The relationship between guanacos and the people of Patagonia goes back more than 10,000 years (Borrero 2001). After the Spanish conquest, and more intensively since the end of the nineteenth century with the consolidation of the Patagonian livestock production model (mostly sheep husbandry), the social perception toward guanaco changed dramatically. The perceptions shifted from the guanaco playing a

The original version of this chapter was revised. The correction to this chapter is available at https://doi.org/10.1007/978-3-031-06656-6_10

N. M. Schroeder (✉)
Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA-CCT CONICET Mendoza), Mendoza, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), Mendoza, Argentina

Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Mendoza, Argentina
e-mail: natalias@mendoza-conicet.gob.ar

V. Rodríguez
Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC-CONICET), Puerto Madryn, Argentina
e-mail: rodrigue@cenpat-conicet.gob.ar

A. Marino
IUCN SSC South American Camelid Specialist Group (GECS), Mendoza, Argentina

Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC-CONICET), Puerto Madryn, Argentina
e-mail: marino@cenpat-conicet.gob.ar

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_3

crucial role in the material and symbolic life of the native people to becoming an obstacle to the livestock activity introduced by the new settlers, mostly European immigrants, who occupied the lands previously usurped by the national state (see Chaps. 2 and 6). Thus, a socio-ecological conflict started, focused on the guanaco as a herbivore competing with livestock for the available forage (Baldi et al. 2010).

After decades of the so-called "sheep colonization" (favored by the international demand for wool during the First World War, relatively simple production processes and high profitability, Coronato 2010), Patagonian sheep husbandry began a process of profound crisis from which it has not recovered. This crisis resulted from the sum of biological factors inherent to highly selective sheep grazing, combined with management actions, i.e., mainly the overestimation of the carrying capacity of pastures and the inadequate distribution of sheep in large and heterogeneous paddocks. Consequently, Patagonian ecosystems underwent a severe degradation process, and sheep stocks experienced negative growth rates (Aguiar et al. 1996; Golluscio et al. 1998; Andrade 2014; Coronato 2010). This scenario was aggravated by other factors, such as wool price fluctuations, volcanic eruptions (Hudson in 1991 and Puyehue in 2011), and severe drought events (Aguiar et al. 1996; Mazzonia and Vazquez 2009). By the end of the twentieth century, the Patagonian steppe reached a high degree of desertification, with no current signs of recovery (del Valle et al. 1998; Oliva et al. 2016). As a consequence of all these processes and the low profitability of sheep, livestock producers reduced their flocks or abandoned their ranches. In southern Argentine Patagonia, by 2015, at least 30,000 km^2 in the Central Plateau of Chubut (Carcamo et al. 2016) and more than 100,000 km^2 in Santa Cruz consisted of abandoned ranches (Oliva et al. 2017).

The livestock husbandry crisis has intensified the conflict with the guanaco over natural pastures in recent years. Some guanaco populations have recently shown signs of recovery, probably due to national and international conservation policies (CITES 2021; Baldi et al. 2006; Nugent et al. 2006) and the abandonment of ranches with their consequent depopulation. Some ranchers identified this recovery as another external factor responsible for the sustained sheep husbandry decline and the fall in profitability (Andrade 2014; Ormaechea et al. 2019). In particular, producers are concerned that the increase in guanaco densities, which is perceived as uncontrolled and over-carrying capacity, leads to a competition for forage resources with livestock and causes overgrazing and habitat deterioration, decreasing

A. Panebianco · F. Peña
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina
e-mail: apanebianco@comahue-conicet.gob.ar; fpena@mendoza-conicet.gob.ar

F. Peña
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina

Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA- CCT CONICET Mendoza), Mendoza, Argentina
e-mail: fpena@mendoza-conicet.gob.ar

rangelands' receptivity. These assumptions, for which there is no scientific consensus, have been used to justify the demands for extractive management. The government of Santa Cruz province has authorized actions to reduce the number of guanacos within ranches and, more recently, promoted changes in national public policies related to guanaco management (see Chap. 6). In this chapter, we evaluate these assumptions through a review and synthesis of the direct and indirect evidence accumulated to date on (1) the competitive interactions between guanacos and livestock for forage resources and (2) the role of the guanaco in the degradation of Patagonian grasslands. This review process allowed us to identify information gaps and provide research and management guidelines to help reduce perceived conflicts that have no ecological basis and mitigate current socioeconomic concerns regarding guanaco population recovery. Our review methods are detailed in Box 3.1.

Box 3.1: Database Search

We conducted an extensive search of the literature and identified studies that compared food and habitat use between guanaco and livestock and the impact of guanaco on vegetation in Patagonia rangelands. We first searched in electronic databases (Scopus, Wiley Online Library, Scielo), internet search engines (Google Scholar), and specialized digital repositories (INTA, SIDALC, MINCYT, CONICET, and Universities from Argentina and Chile) using different combinations of the following keywords: "guanaco," "*Lama guanicoe*," "livestock," "sheep," "cattle," "goat," "horse," "domestic," "diet," "dietary' "food," "feeding," "abundance," "density," "occupation," "distribution," "habitat," "overlap," "segregation," "herbivory," "grazing"). For Google Scholar, we checked for relevance the first 15 hits. We validated our search strategy by testing whether the known relevant papers appeared in the search results. We included peer-reviewed papers, thesis, book chapters, conference proceedings, and technical reports (gray literature). Although this chapter focuses on the situation in Argentinean Patagonia, we also include studies from Chilean Patagonia due to the similarity between environments and to increase the sample size. After removing duplicates of a preliminary list of articles, we applied two filters: (1) a first reading of titles and abstracts to effectively eliminate irrelevant articles and (2) an evaluation of the full version of the article. When the full text was not available online, we contacted specialist librarians and/or authors. For the final selection of articles, we applied general and specific inclusion criteria according to the particular topic under review. Overall, we excluded studies outside Patagonia and review articles. We only considered studies that analyzed diet or habitat overlap among herbivores in the same research. For example, we excluded studies that compared the diet of an herbivore with dietary information of another herbivore from previous different work (e.g., Muñoz and Simonetti 2013). We also excluded studies that did not analyze herbivore diets on sympatry. For example, we excluded studies that compared the diet of one species at one site with the diet of another species at a different site (e.g., Quinteros 2017). Finally, for

(continued)

Box 3.1 (continued)

the review of dietary overlap, we considered only studies that reported some index of similarity in order to facilitate the systematization of comparative dietary information between different studies. Regarding spatial segregation and habitat overlap, we included studies that assessed niche overlap, abundance or traces (feces, footprints), correlations or comparisons, shifts in habitat use, or time series analysis of both guanacos and livestock.

When we detected linked articles (i.e., the same study reported in different formats such as conference abstracts, reports or journal papers, or several journals), we grouped and examined them for eligibility as a single unit. If we found true duplicates, we prioritized those that were peer-reviewed. If the linked articles used the same dataset, but with different analytical approaches, we considered them as a single study.

From an initial list of 222 results from all searches, 115 unique studies remained after the title and abstract filtering stage. However, 2 of these studies could not be obtained in full text for further examination because they were not available in any library consulted and the authors could not be contacted. Following full-text assessment, the final review incorporated 45 studies, 8 on diet (Table 3.1), 20 on habitat use (Table 3.2), and 17 on guanaco impact on vegetation (Table 3.3, Box 3.3).

3.2 Competition Between Guanacos and Livestock: Who Is Excluded?

In extensive grazing systems, whose areas largely overlap with the ranges of wild species, the compatibility of livestock husbandry with the maintenance of the ecological functions of native herbivores represents a recurrent concern for biodiversity conservation and productive development. In this context, the question regarding the interspecific competition between ecologically similar wild and domestic herbivores has guided countless studies worldwide and in diverse ecosystems (Putman 1986; Hobbs et al. 1996; Voeten and Prins 1999; Johnson et al. 2000; Mishra et al. 2004; Young et al. 2005; Ogutu et al. 2010; Du Toit 2011; Odadi et al. 2011; Riginos et al. 2012; Fynn et al. 2016; Schieltz and Rubenstein 2016).

By definition, competition occurs when sympatric species share limited resources (Belovsky 1986; Putman 1996). For two competing species to coexist, there must be a fundamental difference in preferred resources (i.e., niche differentiation, Schoener 1974; Pianka 1974), or shared food should not be limited. If niche differentiation does not occur (or if habitat characteristics prevent it), one of the competing species will eliminate or exclude the other (i.e., competitive exclusion, Hutchinson 1957; Begon et al. 2006). Obtaining evidence of competition in natural situations is particularly challenging for large herbivores with extensive habitat requirements because experimental and manipulative approaches to removing one or more of the competing species are ideally required (Schoener 1983). In this scenario, observed shifts in food and habitat use patterns in exclusive (allopatry) and mixed grazing settings (sympatry) or at contrasting species densities have often been used as an approach to the study of interspecific interactions (Madhusudan 2004; Mishra et al. 2004; Bhola et al. 2012).

The current debate around the guanaco–livestock conflict in Patagonian rangelands focuses on the idea that the guanaco outcompetes livestock for forage. In a context of limited resources, these assumptions imply that competitive exclusion of livestock would be reflected in unfavorable changes in diet and habitat use in the presence of guanacos compared to exclusive grazing situations. The literature review for this section focused on looking for evidence (direct and indirect) on these aspects (Box 3.1).

3.2.1 Food Niche Dimension: Similarity, Variability, and Herbivore Diet Shifts

We reviewed eight ($n = 8$) original studies that compared the diet of guanacos with one or several types of livestock (sheep, cattle, horse, and goat) in Patagonian environments (Box 3.1, Table 3.1). Geographically, the studies were carried out in the extra-Andean Patagonia of Chubut and southern Mendoza provinces ($n = 2$) and zones of ecotone with *Notophagus* forest in Tierra del Fuego, both in Argentina ($n = 4$) and Chile ($n = 2$). The most common type of livestock was sheep ($n = 7$), followed by cattle ($n = 4$), and to a lesser extent horses ($n = 2$) and goats ($n = 1$). Most studies analyzed annual diet similarity of herbivores at different sites or seasons ($n = 7$); only a few included an assessment of herbivore diet shifts in mixed or exclusive grazing settings ($n = 3$, Table 3.1). Four ($n = 4$) papers addressed some spatial or temporal variability in diet similarity indices.

Overall, guanacos and livestock largely overlapped their diets year-round. The highest similarity occurred between guanaco and sheep and the lowest between guanaco and goats (Table 3.1). However, there was considerable variability in diet similarity between sites and seasons for the species considered, although few studies addressed this issue. For example, in the spring season, the dietary overlap between sympatric guanacos and sheep in terms of the percentage of plant functional types varied from 49.1% to 84.4%, depending on the study site (Baldi et al. 2001, Table 3.1). When the overlap was analyzed in terms of key species, which provides greater detail of consumption at the genus or species level, the overlap decreased considerably (Table 3.1). This difference can be important when incorporating dietary overlap in animal equivalent calculations and is lost when grouping by functional group (see Sect. 3.3.2).

Theoretically, in periods of food shortage, similarities in food niches between competing herbivores should be high (Putman 1996). However, a high dietary overlap under sympatric conditions may also be possible when food availability is not

Table 3.1 Main characteristics and results on diet similarity indexes and food niche shifts of guanaco and livestock reported by reviewed studies

Source	Environment/ location	Similarity index	Livestock	Sites	Sp	Sm	A	W	Annual	Analytical approach	Food niche shifts
Baldi et al. (2004)	Steppe of Chubut, Argentina	Kulcyznski's index (plant functional types)	Sheep	1	49.1	77.3				–	–
				2	66.0	78.1					
				3	52.1	76.1					
				6	67.5	93.5					
				7	69.0	89.9					
				9	84.4	75.7					
		Kulcyznski's index (key plant species)		1	39.1	72.3				–	–
				2	58.6	66.6					
				3	44.5	68.8					
				6	67.3	74.4					
				7	65.1	79.0					
				9	66.4	71.3					
Puig et al. (2001)	Steppe of Mendoza, Argentina	Perc. of overlap (O, Hurlbert) (plant species)	Sheep	Sandy					83.0	–	–
			Horse	Rocky					60.0		
				Sandy					76.0		
			Goat	Rocky					48.0		
			Cattle	Sandy					60.0		
				Rocky					53.0		

Pontigo et al. (2020)	Steppe of Tierra del Fuego, Chile	Simplified Morisita's Index (plant species)	Sheep	CG		96.0				Between sites. Mixed/ exclusive grazing sites	Guanaco: significantly lower niche width in mixed grazing setting. Changes in selectivity indexes of not key plant species. Sheep: not evident. Low variation in feeding selectivity among sites.
Bonino and Pelliza (1991)	Steppe/ecotone steppe-forest of Tierra del Fuego, Argentina	Bray and Curtis index (plant species)	Sheep	Steppe					52.0	–	–
				Ecotone					66.0		
			Cattle	Steppe					63.0		
				Ecotone					69.0		
Fernández Pepi et al. (2014)	Ecotone steppe-forest of Tierra del Fuego, Argentina	Sorensen index (plant species)	Cattle	Ranch		70.0				–	–
Fernández Pepi et al. (2018)	Ecotone steppe-forest of Tierra del Fuego, Argentina	–	Sheep, cattle, horse	One ranch (guanaco) Two ranches (mixed)	–	–	–	–	–	Between sites; mixed/exclusive grazing sites	Guanaco: change in the frequency of consumption of different life-forms

(continued)

Table 3.1 (continued)

Source	Environment/ location	Similarity index	Livestock	Sites	Sp	Sm	A	W	Annual	Analytical approach	Food niche shifts
Raedeke (1979)[a]	Ecotone steppe-forest of Tierra del Fuego, Chile	Kulcyznski's index (forage class)	Sheep	NE of the ranch	49.0 (Sep)	80.4 (Dec)	84.7	32.0	67.7	Between seasons; contrasting sheep and guanaco densities	Guanaco: less dietary overlap with sheep, more browsing and less dietary trophic diversity at high sheep densities. Sheep: no significant seasonal change in sheep diet, regardless of the presence/absence of guanacos
					32.4 (Oct)	76.6 (Feb)					
Soler et al. (2012)	Ecotone steppe-forest of Tierra del Fuego, Argentina	Pianka index (plant species)	Sheep	Area within a ranch	52.0	57.0	55.0	72.0	59.0	–	–
			Cattle		58.0	68.0	67.0	59.0	63.0		

Similarity index values are expressed in percentage of overlap (%). References: Sp (spring), Sm (summer), A (autumn), and W (winter) seasons

[a]PhD thesis. The rest of the studies are research papers

limiting (Pianka 1974), and in that case, competition pressure would be low. We found support for both hypotheses in the reviewed papers (Table 3.1). Baldi et al. (2001) found a significantly higher dietary overlap between guanacos and sheep in summer than in spring, at least for key plant species. Compared to spring, in summer, the study sites showed lower plant species richness and a significant decrease in the percentage of living plant tissue (i.e., green) of the herbaceous stratum (perennial and annual grasses and herbs). Thus, the authors concluded that the forage resource for these herbivores in the Central-East region of Chubut province was more limited in summer than in spring, leading to a higher potential for interspecific competition. Similarly, in central Tierra del Fuego (Argentina), Soler et al. (2012) reported that guanacos and sheep overlap their food niche mostly in winter. In this southern part of the continent, spring comes late and occurs slowly and summer is very short. Although plants start growing in spring, peak forage abundance occurs only during the summer (Borrelli and Oliva 2001). Thus, the authors considered that forage availability for herbivores in this area is lower in winter and spring (Soler et al. 2012). A limitation of both studies is that food resources are assumed to be restricted based only on seasonal plant availability, without considering the number of animals of each species feeding at the site. In favor of low competition pressure, Raedeke (1979) found high values of diet similarity between guanacos and sheep in the summer of Tierra del Fuego (Chilean side), when food is abundant and sheep densities are low due to the livestock management.

The analysis of food niche shifts between potentially competing species in mixed and exclusive grazing settings provides an understanding of the competitive effects and may help elucidate which species is more adversely affected by competition for forage. Only three papers out of the total reviewed addressed this issue (Table 3.1). All of them assessed changes in guanaco diet, but only two looked at dietary shifts in livestock. The analytical approaches also differed, following a spatial or temporal focus. Two papers compared diets between sites with and without livestock (sheep, horses, and cattle in Fernandez Pepi et al. 2018, sheep in Pontigo et al. 2020) and with and without guanacos (Pontigo et al. 2020). The remaining study compared guanaco feeding habits between seasons with contrasting sheep densities (Raedeke 1979). All the papers found a change in different dietary parameters of guanacos when grazing alone compared to when sharing habitats with livestock, and none of the papers reported dietary changes in livestock that can be attributed to the presence of guanaco (Table 3.1). Pontigo et al. (2020) reported the widest niche for guanacos where sheep were absent (in a protected area). In contrast, sheep showed low variation in niche width and dietary selectivity indices between sites; moreover, they showed high selectivity for two key dietary species (*Azorella trifurcata* and *Trifolium repens*) at all sites where they were present. Additionally, the authors found that some (not key) plant species avoided by guanacos when grazing alone were selected or at least not avoided at the site they share with sheep (dandelion *Taraxacum officinale*, paramela *Adesmia boronioides*, ryegrass *Lolium multiflorum*). The authors concluded that sheep are indifferent to the presence of guanaco as a potential competitor, but guanaco did seem to be affected by sheep, at least in summer. In addition, differences in diet composition and selectivity between sheep and guanacos in sympatry were smaller than the authors expected. They speculate that it could be related to aspects that they did not measure, i.e., the forage was not limiting or the species were spatially segregated, highlighting the importance of including them in the design of diet comparison studies. Fernandez Pepi et al. (2018) conducted a descriptive analysis of the consumption of different plant life-forms by guanacos in different livestock grazing situations that did not significantly differ in plant composition; i.e., they were comparable. The authors found that guanacos consumed fewer grasses when grazing with sheep and fewer herbaceous dicotyledons when grazing with cattle and horses than when grazing alone. Finally, Raedeke (1979) reported a significant change in the guanaco diet when interacting with sheep. When sheep were present at low densities and coincident with abundant forage (summer), guanaco and sheep had similar diets based mainly on grass and grass-like life-forms. However, when sheep stock density increased up to ten-fold in winter and food availability was reduced, guanacos dramatically changed their diet by increasing their consumption of woody plants, explaining the decrease in dietary overlap at that time (Table 3.1). The dietary trophic diversity of guanacos also declined sharply at high sheep density in winter. These shifts were not observed in guanaco diets on winter ranges without interacting sheep, so the author ruled out that they were due to dietary preferences or a seasonal phenomenon associated with the nutritional quality of browse. Conversely, no significant seasonal change was observed in sheep diet regarding forage class consumption and trophic diversity, regardless of the presence/absence of guanacos. The author concluded the evidence strongly supports the hypothesis that guanaco was more affected by interspecific competition than sheep. The results of Raedeke (1979) suggest that, when the floristic composition of the environments allows it, herbivore densities and forage availability define whether dietary overlap increases or decreases, and both factors could be interacting through the guanaco's dietary flexibility. When the floristic composition limits dietary flexibility (no alternative food), the guanaco would be excluded and spatial segregation would come into play (see Sect. 3.2.2).

According to the few studies assessing changes in food niche, the guanaco is the species that adjusts its foraging behavior when livestock is present but not the opposite. Diet overlap between guanaco and livestock can reach high values but is highly variable between seasons and locations and is further confounded by differences in spatiotemporal use of landscapes by guanaco and livestock. Thus, diet similarity is insufficient by itself to make inferences about interspecific competition. Knowledge of temporal and spatial variability in resource supply, ungulate distributions, and herbivore densities are additional and essential requirements to evaluate the interspecific competition, which were not accounted for in most reviewed studies.

3.2.2 Habitat Niche Dimension: Spatial Segregation and Habitat Shifts

According to the theoretical framework of the competition, under conditions of limited resources, high overlap in one niche dimension between two species is expected to be coupled with high segregation in another dimension (Pianka 1974). For example, when environmental heterogeneity permits it, high diet overlap is often accompanied by high spatial segregation, which allows the two species to coexist without increasing competitive interactions. In this framework, we reviewed the available information on habitat use of guanaco and livestock in mixed grazing situations to assess whether there is evidence of spatial segregation and competitive exclusion. To assess which species get excluded, we also searched for papers that compared the spatial distribution and habitat use of these herbivores in sympatry and allopatry and studies in which the abundance of one herbivore was altered (reduced or suppressed) while the responses of the remaining one were monitored. We identified 20 studies that addressed directly or indirectly the habitat use of guanacos and livestock in Patagonian environments (Table 3.2). The studies were conducted in steppe and austral Monte areas of Chubut (n = 8, mainly in the coastal zone), Santa Cruz (n = 3), Neuquén (n = 2), and Mendoza (n = 3) provinces in Argentina, and Torres del Paine, Chile (n = 1). We also included studies in the steppe-forest ecotone of Tierra del Fuego, Argentina (n = 1) and Chile (n = 3). Livestock reported were mainly sheep but also cattle, horses, and goats in some cases. The methodological approach mainly consisted of population surveys of guanacos and livestock at multiple spatial scales. Some studies also included the analysis of traces, such as feces, footprints, carcasses, etc. Population data were often analyzed concerning variables relevant to herbivore distribution (forage availability, relief, anthropic variables, etc.) generally through generalized linear models or density surface models.

Spatial segregation between the two species was reported in 19 (95%) of the reviewed papers, with guanacos displaced to habitats with lower availability of preferred plant species, less productive, or occurring in underutilized sites or inaccessible to livestock. Conversely, when evaluated, livestock were mainly associated with productive sites or with total plant cover and availability of the preferred plant species in their diet. In cases where the studies included a control situation without livestock (n = 7, Table 3.2), the change in guanaco selection toward the most productive habitat was evident. The process occurred at local or within-paddock, landscape, and regional scales (Table 3.2). In contrast, we found no studies that had control situations without guanacos that assessed changes in habitat use or livestock abundance due to the presence of guanacos.

Factors related to habitat selection and consequent spatial segregation among these herbivores were scale-dependent and consistent among studies. At the landscape or regional scale, guanacos occupied mainly steep terrain, remote and degraded areas, unsuitable for livestock husbandry (Pedrana et al. 2010; Burgi 2012; Antún and Baldi 2020) or areas far from human rural settlements or towns (Schroeder et al. 2013, 2014; Rivas et al. 2015). For example, Pedrana et al. (2010)

Table 3.2 Main characteristics and results on spatial segregation and habitat shifts of guanacos and livestock reported by reviewed studies

Source	Environment/ location	Livestock	Variable analyzed	Controls without livestock	Spatial scale	Spatial segregation	Evidence of competitive exclusion (habitat shifts/ecological release)
Raedeke (1979)[a]	Ecotone steppe-forest of Tierra del Fuego, Chile	Sheep	Abundance	Yes	Between-paddocks/ranch and surroundings	Yes	Guanaco: shift from intensive use of preferred habitats (grassland) to less preferred habitats (forest) when sheep are present (summer and winter); current sheep niche within historical fundamental guanaco niche
Saba et al. (1995)	Austral monte of Chubut, Argentina	Sheep	Signs (feces, tracks)	No	Within-paddock/ranch	Yes	Indirect*; guanacos associated with sites underused by sheep (away from water)
Baldi et al. (2001)	Steppes of Peninsula Valdes, SE of Chubut, and austral monte of Argentina	Sheep	Density	Yes	Between ranches	Yes	Guanaco: increase (by twofold) in density when sheep were removed; densities decreased as sheep stocking rates increased; in sheep-free reserve, density was an order of magnitude higher than at other sites; density inversely related to preferred perennial grass cover and total vegetation cover, which in turn were positively related to sheep density
Puig et al. (1997)	Steppe of Mendoza, Argentina	Small and large livestock	Density	No	Within a protected area	Yes	Indirect; strong negative influence of livestock on the abundance of guanacos, in spite of high food availability
Pedrana et al. (2010)	Steppes of Santa Cruz, Argentina	Sheep	Presence	No	Regional	Yes	Indirect; guanacos associated with less productive sites

Burgi et al. (2012)	Steppes of Peninsula Valdes, Chubut, Argentina	Sheep	Encounter rate	Yes	Protected area and surroundings	Yes	Guanaco: Inter-annual increase in densities when sheep were removed and the ranch was converted into a reserve (ecological release); densities did not vary in neighboring ranches shared with sheep in the same period
Nabte et al. (2013)	Steppe of Chubut, Argentina	Sheep	Encounter rate	No	Between paddocks of different ranches	Yes	Indirect; guanaco encounter rate inversely related to EVI and sheep stocking-rate
Burgi (2012)[a]	Steppes of Peninsula Valdes, Chubut, Argentina	Sheep	Encounter rate	Yes	Regional/ landscape/ local	Yes	Guanacos more abundant in sites without sheep and less productive
Schroeder et al. (2013, 2014)	Steppe of Mendoza, Argentina	Small and large livestock	Co-occurrence/ presence	No	Within a protected area	Yes	Indirect; guanaco negatively related to the probability of presence of small livestock in spring-summer. Livestock: guanaco presence did not explain its occurrence in any season
Moraga et al. (2015)	Ecotone forest-steppe-forest of Tierra del Fuego, Chile	Sheep/ cattle	Density/telemetry	No	Landscape/ local/protected area and surroundings	Yes	
Radovani et al. (2015)	Steppe of Neuquén, Argentina	Goats	Density	No	Landscape/ protected area and surroundings	Yes	

(continued)

Table 3.2 (continued)

Source	Environment/ location	Livestock	Variable analyzed	Controls without livestock	Spatial scale	Spatial segregation	Evidence of competitive exclusion (habitat shifts/ecological release)
Rivas et al. (2015)	Steppe of Mendoza-Neuquén, Argentina	Small and large livestock	Signs (feces, tracks, carcasses)	No	Landscape	Yes	
Traba et al. (2017) and Iranzo et al. (2013)	Steppe of Magallanes, Chile	Sheep/ cattle	Group locations	Yes	Local/protected area and surroundings	Yes	Guanaco: Significant contraction of habitat niche in the presence of sheep during winter (no analogous situation to test for changes in sheep niche) Guanaco and sheep: Tendency (although not significant) for niche contraction with increasing interspecific abundance
Zubillaga et al. (2018)	Steppe/ecotone steppe-forest of Tierra del Fuego, Argentina	Sheep	Abundance	No	Ranch	Yes	
Rabinovich et al. (2018)[b]	Steppe of Santa Cruz, Argentina	Sheep	Distance to nearest neighbor (between guanaco groups)	No	Regional	Yes	
Rodríguez et al. (2018)[b]	Steppes of SE of Chubut, Argentina	Sheep	Density	No	Within-paddock/ranch	Yes	Indirect; guanacos associated with sites underused by sheep (away from water)

Flores et al. (2020)	Steppe of Tierra del Fuego, Argentina	Small and large livestock	Abundance/ productivity (number of offspring/adult)	No	Landscape	No	Indirect; guanaco productivity increased with mesic grassland surface as livestock level and distance to the ranch buildings decreased
Antún and Baldi (2020)	Steppes of Peninsula Valdes, Chubut, Argentina	Sheep	Density	Yes	Landscape	Yes	Guanaco: increase (by threefold) in guanaco density in areas without sheep, compared to sheep ranches; guanacos associated with less productive sites
Marino (2017)[c]	Steppe of Chubut, Argentina	Sheep	Density	Yes (temporal)	Protected area	Yes	Inter-annual increase in densities when sheep were removed and the ranch was converted into a reserve (ecological release)
Marino et al. (2020)	Steppes of Santa Cruz, Argentina	Sheep and cattle	Animal units (AU)	No	Regional	Yes	Indirect; 50–75% of the guanacos estimated for Santa Cruz would be occupying livestock-free abandoned ranches

*Indirect evidence of competitive exclusion is considered when the study does not include a control treatment that can rule out other possible explanatory factors of herbivore habitat use (habitat characteristics, food preferences, human activity, etc.)
[a]PhD thesis; [b]Conference proceedings; [c]Technical report. The rest of the studies are research papers

found that areas with a low probability of guanaco occurrence concentrated in the south of Santa Cruz province, where productive habitats abound. Conversely, the areas with a medium to high probability of guanaco occurrence clumped around the "central high plateau," considered the least productive steppe in the whole region, where severe degradation affects 77% of the land and most ranches were abandoned (Gonzalez and Rial 2004; Borrelli et al. 2004). Antún and Baldi (2020) showed that in areas without sheep in Peninsula Valdés (Chubut province), guanaco density almost triples compared to sites where both species were present. At lesser scales, in areas where guanacos occur in sympatry with domestic herbivores, guanacos showed strong negative relationships with domestic stocks (Raedeke 1979; Baldi et al. 2001; Nabte et al. 2013). Lastly, Saba et al. (1995) and Rodriguez et al. (2018) reported a complementary distribution pattern at a local scale (within-paddock) between guanacos and sheep regarding distance to water sources, suggesting that trophic competition between them may be attenuated by the spatial displacement of guanacos to paddock areas underutilized by sheep.

In the context of temporal dynamics, based on a 41-year data series on a ranch in Tierra del Fuego (Chile), Zubillaga et al. (2018) found that guanaco abundance was inversely related to sheep abundance. In this regard, it is worth noting the complementary trajectories of guanaco and livestock numbers since the beginning of livestock husbandry in Patagonia at the end of the nineteenth century (Box 3.2). These results, consistent at different spatial and temporal scales, support the hypothesis of competitive exclusion for forage of guanacos by livestock, although that of direct harassment by humans cannot be ruled out. The study concluding on the relative importance of both effects (Antún and Baldi 2020) indicates that competitive exclusion for forage would be the determinant of spatial segregation, reinforced by the effect of hunting or harassment by humans.

The most conclusive evidence for competitive exclusion consists of the niche expansion of one species population after the total or partial removal of its competitor (Sheppard 1971; Pianka 1974; Krebs 1978). This process, known as "ecological release," was observed when the conversion of sheep ranches into wildlife reserves was documented (Burgi et al. 2012; Marino 2017) or when changes in livestock stocks were carried out in some paddocks (Raedeke 1979; Baldi et al. 2001). The study of Burgi et al. (2012) is of particular interest because it compared changes in guanaco densities after creating the San Pablo de Valdes reserve (Chubut province) with a control situation of neighboring ranches with mixed grazing of guanaco and sheep over the same time period. Their results showed that guanaco density tripled within 3 years since sheep removal, whereas it remained relatively constant in the surrounding ranches.

Finally, only two of the available papers assessed the effect of guanaco on livestock, neither of which found significant effects. Using an analytical approach, Schroeder et al. (2013) reported that the probability of guanaco presence did not explain the habitat use of large (cattle and horses) or small (goats and sheep) livestock in any season. In contrast, the presence of guanacos was inversely related to the probability of the presence of small livestock in spring–summer. Traba et al. (2017) found a trend of niche reduction of both guanacos and sheep with increasing interspecific abundance. The authors interpreted this result as an apparent density-dependent niche contraction, although the models were not statistically significant. However, they found a large and significant contraction of the guanaco habitat niche in the presence of sheep during winter compared to their niche in allopatry.

Thus, abundance and distribution patterns assessed at variable spatial and temporal scales are in accordance with the spatial displacement of guanacos due to competitive exclusion by livestock, with the former usually occupying areas underutilized or free from domestic herbivores, which in turn seem to be unaffected by guanacos.

Box 3.2: Timeline of Guanaco and Livestock Numbers in Argentine Patagonia

The massive introduction of sheep, and to lesser extent cattle, at the end of the nineteenth century in Argentine Patagonia reached about 20 million heads in 50 years. From then on, during the period 1950–2000 stocks decreased markedly and steadily until they remained relatively stable at around 8 million at the end of the twentieth century (SENASA, INDEC, Argentine Wool Federation, Fig. 3.1).

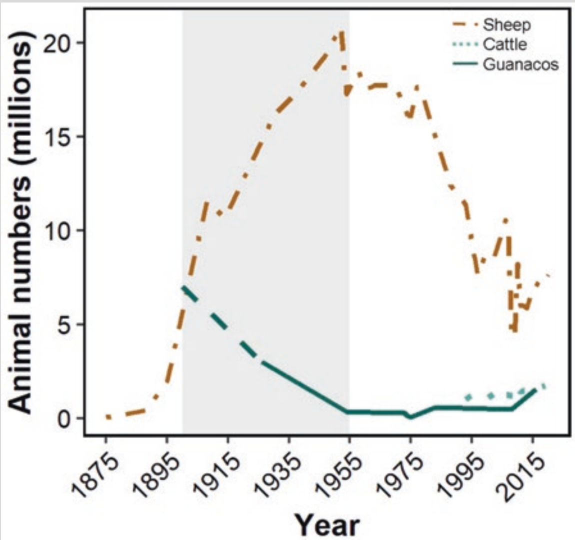

Fig. 3.1 Trend of domestic stocks and estimated guanaco numbers over time in Argentine Patagonia. Estimated guanaco numbers are from Argentina (Raedeke 1979; Torres 1985; Baldi et al. 2016; González y Acebes 2016), except for 1900 which is for South America (Torres 1985, hence the dotted lines in the series). Livestock numbers were obtained by summing up the data available for Mendoza, Neuquén, Rio Negro, Chubut, Santa Cruz, and Tierra del Fuego provinces (SENASA, INDEC, Argentine Wool Federation: https://www.flasite.com/index.php/es)

(continued)

Box 3.2 (continued)

The original guanaco population during the pre-Hispanic period was estimated at 30–50 million animals (Raedeke 1979), declining dramatically during Spanish colonization to approximately 7 million animals in the early 1900s (Torres 1985). Given that the guanaco population had already experienced a range reduction to 40% by that time and Patagonia was just beginning the period of heavy sheep colonization, it could be considered that an important part of those 7 million would be in Patagonia. In Argentina, which hosts 81–86% of the total population, guanaco abundance estimates showed a steady decline until the 1970s, reaching critical situations (70,000 animals in 1975, Raedeke 1979). Subsequently, the guanaco began a slow recovery process that, with varying intensity, continues to date (Raedeke 1979; Torres 1985; Baldi et al. 2016; Gonzalez and Acebes 2016; Carmanchahi et al. 2019, Fig. 3.1).

The historical comparison of domestic stocks in Argentine Patagonia and the approximate estimates of guanaco numbers during the same period (Fig. 3.1) shows that the "sheep boom" coincides with the most dramatic drop in guanaco population values. Subsequently, during the period of greatest sheep decline, guanaco abundances remained at considerable low values (Fig. 3.1). Hence, there is no evidence to hold the guanaco accountable for the past reduction of sheep, which was mainly due to the well-documented unsustainable management (Golluscio et al. 1998; Aguiar et al. 1996). It is unlikely that in recent decades this trend has reversed, and guanaco abundance has suddenly increased, reducing sheep forage. It is more plausible to posit that guanaco populations, which are adapted to live in environments of low-quality forage taking advantage of sites not used by livestock (Sect. 3.2), are progressively occupying expanded degraded and abandoned land that can no longer support the number of sheep they once did (Marino et al. 2020).

3.2.3 Do Guanacos Outcompete Livestock?

The ecological evidence from this section on the shared diet and habitat use between guanacos and livestock, mainly sheep, supports the theoretical predictions of competition for limited resources between herbivores with similar feeding strategies (Schoener 1974; Pianka 1974; Belovsky 1986). However, guanaco rather than livestock seems to be most adversely affected by this interaction. Even though diet overlap can be high in certain situations, consistent spatial segregation and opposite trends in herbivore abundances across spatial scales indicate that guanacos and livestock do not occupy the same habitats nor access the same foraging resources equally. Thus, reporting the total densities of herbivores in sympatry without accounting for their spatial distribution, as well as diet similarity without information on the degree of resource limitation, do not inform competition. Interspecific competition is frequently highly asymmetric; i.e., the consequences are often not the same for both species (Begon et al. 2006). The negative association of guanacos with preferred forage or plant productivity and the changes in diet and habitat use when livestock are absent or removed provides evidence that guanaco is excluded from the preferred habitat in the range shared with livestock. Human disturbances associated with livestock management probably reinforce this exclusion. Conversely, none of the studies examined at full text reported significant effects of guanaco on livestock. Hence, we conclude that, to date, insufficient empirical and ecological data exists, either observational or manipulative, to conclude that guanaco outcompetes livestock in the Patagonian grasslands. On the contrary, the evidence in favor of competitive exclusion of the guanaco is consistent at variable spatial scales, locations, and methodological approaches. Furthermore, the available evidence agrees with the idea of the included niche (Hutchinson 1957), in which livestock realized niche is clearly included within the ideal niche of the guanaco, as outlined by Raedeke (1979). This confirms that guanaco and sheep can coexist because guanacos occupy the niche portions that do not overlap significantly with those of livestock. Thus, under resource distribution heterogeneity, rangelands carrying capacity for guanacos must be higher than that for livestock and not the same, as currently assumed. One of the crucial management implications of this fact is that the underestimation of environmental carrying capacity leads to an underestimation of the supposed overpopulation thresholds and, according to the current management paradigm, would result in inflated harvest quotas.

3.3 Overgraze or Not Overgraze? That's the Question

3.3.1 Impact of Guanaco on Vegetation

In extra-Andean Patagonia, vegetation and soil degradation due to overgrazing are some of the main environmental problems and major causes of desertification. In these environments, livestock production has been strongly associated with unsustainable management practices (Golluscio et al. 1998). Particularly, overgrazing by sheep has been widely reported and is pointed out as the principal cause of the deterioration of the vegetation and the environment by reducing the total vegetation cover, the availability of forage plants in general, and perennial grasses in particular. Sheep grazing leads to changes in the size and spatial distribution of perennial grasses, a reduction in species richness, and an increase in erosive effects on the soil (Bertiller and Bisigato 1998; Chartier and Rostagno 2006; Pazos et al. 2007). Several studies have also reported a negative effect of sheep grazing on early stages of vegetation regeneration, reflected in changes in the soil seed bank (e.g., Bertiller and Bisigato 2005; Pazos and Bertiller 2008; Franzese et al. 2015) and seedling emergence and establishment (Defossé et al. 1997; Bisigato and Bertiller 2005). These effects result from direct consumption of vegetative and reproductive plant tissues and trampling, which in turn can lead to a positive feedback process between increasing disturbance intensity and decreasing regeneration potential (Pazos and Bertiller 2008; Bisigato and Bertiller 2004).

From the livestock management perspective, the guanaco has been blamed for overgrazing and for being responsible for the degradation of Patagonian environments over the last two decades. This claim has been promoted by sectors linked to livestock production and is based mainly on the perception of uncontrolled guanaco population growth exceeding the carrying capacity of rangelands due to the lack of predators and on the observation of guanacos grazing in degraded areas (Marino and Rodriguez 2016; Oliva et al. 2019).

Despite the significance of this claim, few studies have addressed this problem. For extra-Andean Patagonia, we reviewed 13 scientific publications that studied the impact of guanaco on vegetation (Table 3.3). The geographical coverage of these studies focused mainly on the NE of Chubut province, with sedentary guanaco populations. A particular case addressed by four studies involves the *Nothofagus* forests in Tierra del Fuego Island, the only site where guanacos have been documented using these ecosystems. Given its uniqueness, we show the analysis of the information regarding this situation in a specific section (Box 3.3).

For extra-Andean Patagonia, we first classified the studies into two groups, those with direct measurement of vegetation and/or soil ($n = 10$) and those that inferred impact from the relationship between guanaco densities and the estimated carrying capacity of the rangelands ($n = 3$). Among the papers with direct measurements, seven of them found no impact of guanaco grazing on the grasslands, one was not conclusive, and the other two concluded that the observed effect would not compromise the integrity of those grasslands. In addition, four of these studies compared the effects of guanaco and sheep grazing.

The studies by Marino et al. (2016), Pazos et al. (2017), and Marino and Rodríguez (2017, 2019) found that the temporal dynamics of the vegetation for the different plant communities evaluated respond to climatic variability even in areas with high guanaco densities and do not show signs of degradation due to overgrazing. Furthermore, Marino et al. (2016) and Marino and Rodríguez (2017) found that guanaco densities remain stable below the carrying capacity estimated from grass biomass, although other studies demonstrated that this is an underestimate of the actual carrying capacity as the animals consume a significant proportion of non-grass species (Rodríguez et al. 2019). These studies used data collected from vegetation surveys in the San Pablo de Valdés reserve, NE Chubut province, and included simultaneous time series for vegetation dynamics, guanaco density, and climate records for 12 years (the complete series will be included in Pazos et al., in preparation). In this protected area, predation pressure on guanacos is negligible and results from the sporadic presence of pumas (*Puma concolor*, D'Agostino 2018). Considering that guanacos exhibit high territoriality linked to their mating system (Franklin 1983) and the typical dispersal conditions that operate in most of Patagonia, results from these studies suggest that the relationships between forage quantity and guanaco territorial behavior result in a limitation of population density below the values predicted by food availability. This leads to a relatively moderate and homogeneous grazing, independent of predation pressure. Accordingly, herbivory pressure was higher in areas grazed by nonterritorial bachelor groups than in areas grazed by territorial family groups. However, the inter-annual mobility typical of bachelor groups allowed detection of vegetation recovery after these groups left the site (Marino and Rodríguez 2019).

Table 3.3 Main characteristics and results about the impact of guanacos on Patagonian rangelands reported by reviewed studies

Source	Grazing type	Location	Measurement on vegetation	Comparison between types of grazing	Evaluated stock/CC	Grazing impact	Key results
Pazos et al. (2017)[d]	Guanacos	Chubut, Argentina	Yes	No	No	No	Vegetation dynamics respond to climate variability and not to guanaco density
Marino et al. (2016) and Marino and Rodriguez (2017)	Guanacos	Chubut, Argentina	Yes	No	No	No	Guanaco density stabilizes below carrying capacity mechanism of population self-regulation
Burgi et al. (2012)	Guanacos	Chubut, Argentina	Yes	Yes, sheep	No	No	Better vegetation status in guanaco grazing sites compared to sheep grazing sites
Marino and Rodriguez (2019)	Guanacos	Chubut, Argentina	Yes	Guanacos' family groups, guanacos' bachelor groups	Yes	No	Higher intensity of use on sites with guanaco bachelor groups
Oliva et al. (2019)	Total herbivores (guanacos + livestock)	Patagonian region	No	Yes, livestock	Yes	Yes	Total herbivore stock exceeds Patagonia's carrying capacity
Marino et al. (2020)	Guanacos	Patagonian region	No	Yes, livestock	Yes	No	Areas with livestock are overstocked, areas with a high density of guanacos are not
Suarez et al. (2009)[c]	Guanacos	Santa Cruz, Argentina	Yes	No	Yes	No	There is no evidence of grassland degradation
Massara Paletto et al. (2019)[c]	Guanacos	Chubut, Argentina	Yes	Yes, sheep	Yes	Partial*	Lower ANPP at a site grazed by guanacos compared to another site grazed by sheep; no differences for other two sites evaluated

(continued)

Table 3.3 (continued)

Source	Grazing type	Location	Measurement on vegetation	Comparison between types of grazing	Evaluated stock/CC	Grazing impact	Key results
Pecile (20v19)[a]	Guanacos	Chubut, Argentina	Yes	Yes, sheep	No	Yes*	Reduced seedling emergence and vegetative growth compared to enclosures
Oliva et al. (2020)	Total herbivores (guanacos + livestock)	Chubut, Santa Cruz, Argentina	No	Yes, livestock	Yes	Yes	Herbivore overstocked at the ranch scale
Cepeda (2015)[b]	Total herbivores (guanacos + livestock)	Santa Cruz, Argentina	Yes	No	Yes	Not conclusive	Signs of degradation as a result of sheep grazing history
Oliva (2015)[b]	Guanacos	Santa Cruz, Argentina	Yes	No	Yes	No	There is no evidence of grassland degradation; one of eleven communities assessed showed high grazing intensity
Saba et al. (1995)	Guanacos	Chubut, Argentina	Yes	Yes, sheep	No	No	Improved vegetation status at guanaco grazing sites

References: *CC* carrying capacity, *ANPP* aboveground net primary productivity
*The enclosures used in this work excluded all large and medium-sized herbivores present at the sites, making it difficult to interpret the results
[a]Msc thesis; [b]Workshop proceedings; [c]Technical report; [d]Book chapter. The rest of the studies are research papers

Box 3.3: The Impact of Guanacos on the Regeneration of Native Forests

The guanaco's main natural habitat comprises open environments, such as grasslands and shrublands (Raedeke 1979). However, in Tierra del Fuego Island (54°21′43″ S; 67°38′17″ W), in the Southern tip of Patagonia, a distinctive situation occurs in which the species also uses native *Nothofagus* forests. This behavior seems restricted to this area, as this herbivore has not been recorded entering the forest in the continental part of Patagonia. One of the typical environments of the so-called Ecotone Zone on the Island, and frequently used by this herbivore, is the lenga forests (*Nothofagus pumilio*), a tree of timber importance, adjacent to wetlands (Quinteros 2014; Dodds 1997). Guanacos and *Nothofagus* forests have coexisted and co-evolved for thousands of years (Sarno et al. 2001). However, the establishment of livestock ranches initially dedicated to sheep husbandry, the increase in cattle ranching and forestry, together with fencing, and the development of cities, roads, and other communication routes have altered the natural landscape in which guanaco populations and forests naturally coexisted (Franklin 1982; Raedeke 1982; Schiavini et al. 2009). Recent studies have suggested that high sheep densities in the area reduced the forage available to guanacos and promoted a more intensive use of the forests, leading to concern in the forestry sector about the impact of the guanaco on browsing (Raedeke 1982; Moraga et al. 2014).

We reviewed four original studies that estimated the potential impact of guanaco in Patagonian forests in Tierra del Fuego Island. Two of them were conducted in the Argentinean portion (Pulido et al. 2000; Quinteros 2014), while the other two, in Chile (Cavieres and Fajardo 2005; Martinez Pastur et al. 2016). These studies reported that the presence of guanaco in lenga forests had been associated with browsing damage in some aspects of the regeneration of these environments (Quinteros 2014; Pulido et al. 2000). This impact has been evidenced in primary and harvested forests on the Argentinean and Chilean sides of Tierra del Fuego Island (Pulido et al. 2000). The main impacts are related to browsing damage and a decrease in growth, reflected in shorter trees and changes in shape (Pulido et al. 2000; Cavieres and Fajardo 2005; Quinteros 2014). Other signs of herbivory, such as modifications in the understory, soil, or abundance of saplings, have not been reported (Quinteros 2014). While these impacts could have negative consequences on forest regeneration, the researchers highlight the need to study these effects at larger temporal and spatial scales, which would allow understanding of the scale of the problem and its implications in forest dynamics.

Box 3.3 (continued)

More recently, Martinez Pastur et al. (2016) studied the effect of exclosures as a control measure for browsing damage and found that while exclosures did not influence regeneration density, they did have positive effects on growth and tree quality, with consequences for the management of these forests. This work highlights the importance of considering environmental conditions like climatic factors, which can have a synergistic effect on herbivore browsing.

To achieve good management practices, a good monitoring program of both guanaco populations and lenga forests is needed to ensure the conservation of the species and the proper management of the forests. Moreover, it should include studies at several scales (e.g., patch-level, landscape-level) and the potential competition with domestic herbivores to achieve a better understanding of the dynamics of these ecosystems.

In Santa Cruz province, Suarez et al. (2009) reported positive trends in variables reflecting vegetation status obtained from fixed monitoring of 11 vegetation communities in Monte León National Park for the 2005–2009 time period. The authors concluded that the grasslands showed no evidence of overgrazing even though the density of guanacos would exceed the estimated carrying capacity of the park. At the same site, Oliva (2015) reported the results of a third survey carried out in 2015, in which they found that the trends remained positive or stable and that the park was moderately grazed, except for one graminoid community where they recorded low forage productivity and high grazing intensity. Both reports evince the inconsistency between moderate grazing and vegetation status with the estimated supposed herbivore overstock. However, the authors calculated the carrying capacity of this park using a method developed for livestock, using sheep consumption parameters and based on a weak estimate of guanaco abundance in the park. This would lead to an underestimation of forage availability and an overestimation of the guanaco population within the park (Marino and Rodríguez 2016).

The studies by Burgi et al. (2012), Saba et al. (1995), Massara Paletto et al. (2019), and Pecile (2019) compared the vegetation status between sites with guanaco grazing and with sheep grazing or mixed grazing (guanacos and sheep). In the first two studies, the authors reported higher values of total cover and forage species (particularly perennial grasses) in the sites with guanaco grazing (Saba et al. 1995; Burgi et al. 2012). Burgi et al. (2012) also highlight the rapid recovery of the plant communities in terms of botanical composition and vegetation cover after the removal of sheep, despite the increase in the guanaco numbers. The study by Saba et al. (1995) is particularly interesting because it assessed vegetation status within the same paddock, identifying sites with guanaco or sheep grazing based on their density and spatial distribution (see Sect. 3.2). For a shrub-grass steppe, Massara Paletto et al. (2019) found a marginal positive difference in the aboveground net primary productivity (ANPP) of the site with mixed grazing compared to an adjacent one with guanaco grazing and with exclosures installed at both sheep and guanaco grazed sites. However, this pattern was not observed in two other sites included in this study (one in Peninsula Valdes and the other in Austral Monte), nor for the production of forage species. The authors suggest that the contrasting results between ANPP and forage species from the shrub–grass steppe would be a consequence of a more homogeneous distribution of grazing pressure on vegetation observed in terms of the species consumed in areas with guanaco grazing. Pecile (2019) found no differences in grassland sexual regeneration, botanical composition, or spatial distribution of seedlings between mixed grazing sites and sites grazed by guanacos. However, in sites with mixed grazing, the exclusion of herbivores improved seedling emergence and the vegetative growth of the dominant perennial grass species. The studies by Massara Paletto et al. (2019) and Pecile (2019) resulted from joint sampling using exclosures that also excluded other herbivore and granivore species (e.g., *Rhea pennata*, *Eudromia elegans*, *Dolichotis patagonum*). In addition, in the mixed grazing sites, it was not possible to identify the intensity of vegetation used by the different herbivore species. Thus, we consider that these two conditions hinder the interpretation and validity of some results and conclusions.

In Santa Cruz province, Cepeda (2015) conducted a grassland survey, which started in 1991 and estimated the receptivity, vegetation status, and total herbivore stock (sheep + guanacos since 2007) in a ranch next to the Monte León National Park. The author concluded that the current state and condition of the grasslands could not be attributed to the guanaco alone, as there is a degree of degradation due to sheep grazing before the increase in guanaco population that could not be reversed by the livestock management practices implemented.

The guanaco has anatomical, physiological, and behavioral adaptations that would cause lower impact grazing than domestic livestock. Among the most important adaptations is the high efficiency of nitrogen cycling in the rumen, which allows it to make better use of forage (Schmidt-Nielsen et al. 1957; Livingston et al. 1962). In turn, this enables it to incorporate items of little or no forage value compared to livestock consumption, such as *Hyalis argentea* in Chubut (Rodríguez et al. 2019; Massara Paletto et al. 2019) or *Stipa* sp. and *Festuca* sp. in Santa Cruz (Marino 2017). In addition, guanacos have plantar pads that attenuate the impact of trampling (Wheeler 1995). These adaptations supplement the already described mechanism of population self-regulation (Marino et al. 2016). The eventual differences in grazing impact between guanacos and livestock species highlight the importance of assessing their spatial distribution in order to identify which species (type and density) uses a particular area within the management unit of interest. This concept is fundamental at both the between-paddock (Burgi et al. 2012) and within-paddock (Saba et al. 1995, Marino and Rodríguez in preparation) scales.

Among the three studies that analyze the impact of guanacos on vegetation based on the relationship between guanaco densities and the carrying capacity of grasslands, two infer overgrazing by guanacos (Oliva et al. 2019, 2020) and one does not (Marino et al. 2020). The three papers are related as they constitute one original publication and two replicates; they share some of the information but with different approaches (Oliva et al. 2019, 2020; Marino et al. 2020). In the first paper, Oliva et al. (2019) postulated that the total herbivore stock for extra-Andean Patagonia is above carrying capacity, estimated from a method based on remote sensing. These authors posit that the stock of domestic herbivores declined to values close to grassland receptivity during the last decades. However, the recovery of guanaco populations would have caused the total herbivore stock to exceed this receptivity, threatening the integrity of the rangelands and the productive potential of livestock husbandry in the region. Based on the information reported in this study, Marino et al. (2020) cautioned that the spatial distribution of guanacos and livestock had not been considered in the analysis and that these species show a marked pattern of spatial segregation (see Sect. 3.2), which would completely modify the results of the relationship between herbivore stock density and carrying capacity. This new analysis showed that the risk of overgrazing is evident in the areas with the highest stock of domestic herbivores but not in the areas where most of the guanaco populations are concentrated. In the third paper, Oliva et al. (2020) persisted in the findings associated with herbivore overstocking, showing results for 13 ranches located in Santa Cruz province. The authors analyzed the stock density and receptivity at the ranch scale (for each establishment) without direct measurements on the vegetation and omitting the intra-ranch spatial distribution of herbivore species. The controversies between these studies arise mainly from the approach and the methodology applied. The analysis by Oliva et al. (2019) uses an agronomic approach considering global stocks, animal equivalents based only on body weight, and regional estimates of the carrying capacity of grasslands. However, Marino et al. (2020) propose that, given that these are mixed grazing systems that include a wild species, ecological aspects of the guanaco and its interaction with livestock cannot be ignored. In addition, they stress the critical importance of drawing conclusions based on empirical information that is as direct as possible. In this sense, vegetation and soil measurements as well as clear and consensual criteria to determine environmental impact due to overgrazing are fundamental.

In summary, relatively few studies have addressed the impact of guanacos on vegetation, and most report no evidence that guanaco grazing poses a threat to rangeland integrity. In general, guanaco grazing was moderate compared to sheep grazing, possibly due to adaptations resulting from the co-evolution of these wild herbivores and the Patagonian environments. Also, based on this review, we identify the need to broaden the geographical range to incorporate other environments and to include temporal variability.

3.3.2 On the Carrying Capacity Assessment

Carrying capacity or receptivity assessment is used to prevent rangeland degradation and/or to achieve production goals. It is computed by relating the estimated availability of consumable forage (kg dry matter/km^2), a forage use factor for herbivores (i.e., the percentage of available forage that can be consumed under a sustainability assumption) and the annual requirement of an average adult animal of a given species (kg dry matter/year, Johnston et al. 1996). Current methods for estimating Patagonian carrying capacity for livestock assume, a priori, a grazing distribution proportional to forage availability, which usually differs between plant communities within paddocks and omits any other factor that could account for the spatial distribution of animals (Massara Paletto and Buono 2020). These same methods are being used to estimate joint carrying capacity for guanaco and livestock in order to evaluate overgrazing risk or derive guanaco harvest quotas in response to culling demands. In these cases, the available methods include guanaco numbers through animal equivalents that assume a complete dietary overlap (100%) and simple live-weight relationships. Rangeland receptivity is associated not only with each herbivore's preference for plant species (consumable forage) but also with whether animals have access to them. The spatial segregation between guanacos and livestock found consistently at different spatial scales in this review indicates that both herbivores are found in different habitats and therefore do not have equal access to available forage. At the intra-ranch scale, sheep distribution could be affected by some environmental variables such as distance to drinking sites, terrain slope, topography, distance to fences (Ormaechea et al. 2018), and nonnutritional structural factors of vegetation (Bertiller and Ares 2008). These limitations imply that the area of the paddocks that extends beyond the distance that sheep can travel has reduced or no receptivity for them, regardless of forage availability (Saba et al. 1995; Rodríguez et al. 2018). In arid regions, and particularly in the dry season, the distance from water sources may be the variable with the most influence on the shape and size of the animals' grazing area (Trash and Derry 1999) as it determines a gradient of stocking pressure that translates into a gradient of rangeland use (piosphere). Consequently, there is an inverse gradient of forage not consumed by livestock that can be used by other herbivores with fewer water restrictions and capable of occupying these areas (Trash and Derry 1999). In turn, guanacos are limited in their distribution by the presence of livestock and the associated human activity, being able to access the forage that livestock do not use. In this way, it would be livestock management through changes in ranch infrastructure and/or grazing systems, rather than the presence of wild herbivores, the main factor defining an increase in the amount of forage usable by livestock. The guanaco can access any palatable species over 75 cm above the ground level, while sheep cannot (Raedeke 1979), and it may also feed on species of low or null forage value for livestock (Puig et al. 1997; Somlo 1997; Massara Paletto et al. 2019; Rodríguez et al. 2019). Even though guanacos and livestock are expected to forage together in certain contexts, such as during periods of high forage availability (mainly pulses of annual plant species) or in locations where only one species has exclusive access to certain forage items, the gradient of unconsumed forage by domestic animals may explain the observations of both species grazing together in less obvious situations. Therefore, a realistic and efficient estimate of joint carrying capacity for multi-herbivore grazing systems must necessarily take into account these ecological differences between species. A better proposal should focus on adjusting animal equivalents for the

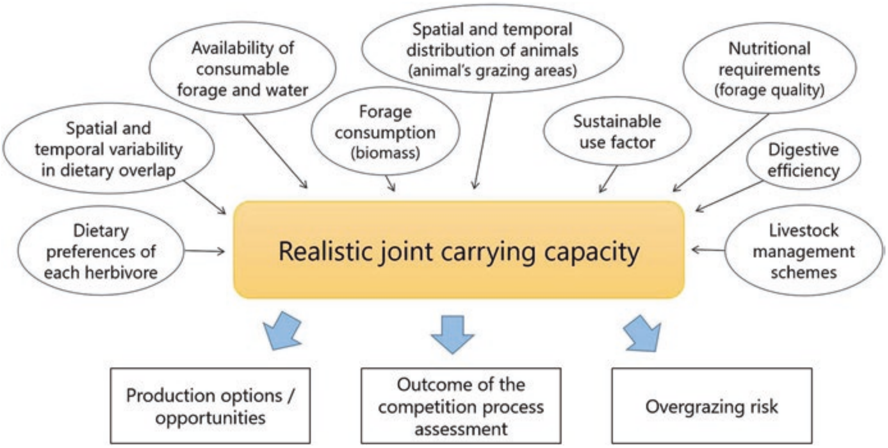

Fig. 3.2 Factors that need to be considered when assessing joint carrying capacity for multi-herbivore grazing systems in arid and semi-arid lands. These considerations would directly influence the outcome of the competition process assessment, the productive opportunities, and the overgrazing risk

significant spatial and temporal variability in the dietary overlap between guanacos and livestock or incorporating all guanaco dietary items and calculating environmental receptivity for the area actually used by each herbivore (Rodríguez et al. in preparation). These considerations would directly influence the outcome of the assessment of the competition process and optimize the adjustment of stocking rates for domestic animals, taking into account whether they are intended to achieve production objectives based solely on livestock husbandry or oriented to a mixed production scheme (Fig. 3.2).

Other ecological parameters have a direct impact on joint carrying capacity calculations that require further research and consensus (Fig. 3.2). As mentioned previously, South American camelids have anatomical and physiological adaptations that give them greater digestive efficiency when compared to other ruminants (Schmidt-Nielsen et al. 1957; San Martín and Bryant 1988; Dittmann et al. 2014). In this sense, the guanaco's daily requirement expressed as dry matter biomass should be less than 3%, which is generalized for ruminants and used to compute animal equivalents dealing with guanaco management. At present, there is a consensus on using 2% of the body weight as the daily requirement of a guanaco, expressed as dry matter biomass based on San Martín and Bryant (1988) estimates (Marino and Rodríguez 2016). On the other hand, guanaco body weight varies geographically (between populations) and according to sex and age categories (within a population), so it would be appropriate to estimate an average weight for the site of interest. Finally, the proportion of grassland vegetation that can be consumed by herbivores in a sustainable way (use factor) that is usually used in livestock management is 30% of ANPP (Holechek et al. 1989), or a value proportional to it (Oliva et al. 2019). However, as the floristic composition and proportion of forage and non-fodder species vary from one environment to another, using a single percentage of total productivity could result in different grazing pressures on forage species (Golluscio et al. 2015). Given the evidence documented in this chapter regarding the low impact of guanaco on rangelands, it is expected that guanaco abundance involving more than 30% consumption would not deteriorate the environment and therefore would not imply overgrazing (Marino and Rodríguez 2016).

Overall, the considerations presented in this section point to a systematic underestimation of the environmental carrying capacity for guanacos when estimated by the methods available for livestock. Therefore, a discussion and consensus are needed to establish clear and straightforward criteria and thresholds to define overgrazing and the risk of grassland degradation based on the characteristics of the environments. Finally, accounting for intra- and inter-annual variability in forage and water supply is essential to estimate the carrying capacity of arid and semi-arid ecosystems and the corresponding uncertainty, as well as to develop management practices and policies (Ellis and Swift 1988; Vetter 2005) including sustainable management of herbivore populations.

3.4 Importance of Ecological Knowledge to Guide Management Decisions

Our review found no ecological evidence to support the claim that guanaco reduces forage availability for livestock nor that guanaco populations threaten the integrity of rangelands and livestock production. Hence, interventions aimed at reducing guanaco populations, such as those promoted in recent years at the provincial and national levels (see Chap. 6), will hardly contribute to improving livestock production. On the contrary, reductions of guanaco populations under the perception of benefits to livestock grazing continue to generate false expectations of a solution for ranchers, in addition to threatening a native species. Given the high diversity of environments and livestock management schemes (extensive production under continuous grazing, rotational grazing, ranches divided into winter and summer ranges, pastoralism, etc.) across the guanaco distribution range, as well as the sedentary or migratory nature of their populations, further studies are required to validate the scope of present conclusions. However, it is evident that, unless traditional livestock management practices are modified, the current factors leading to rangeland degradation and production losses (i.e., grazing heterogeneity and livestock overstock, Golluscio et al. 1998; Aguiar et al. 1996; Andrade 2014) will continue to operate (Marino et al. 2020), irrespective of the reductions in guanaco numbers. Regarding decisions on guanaco management, methods for estimating carrying capacity deserve a special mention. A consistent result that emerged across previous sections from different perspectives, such as diet selection, habitat use, and grazing impact, was the underestimation of environmental carrying capacity for guanacos when computed under the assumptions of the current management paradigm and the available methods, only developed for livestock. This bias has crucial implications since both overgrazing risks and supposed overpopulation thresholds are computed on its basis, after accounting for the forage that would be necessary for the domestic herbivores present in a given ranch. Thus, according to the models recently implemented in Southern Provinces (Williams et al. 2014; Rabinovich 2017), this underestimation of the available food for guanacos results in inflated harvest quotas and unreliable viability assessments. Since management schemes without sound evidence risk leading to undesirable outcomes, new integrated management approaches are urgently needed that consider key ecological aspects with a direct impact on the assessment of overgrazing risk and the development of productive diversification initiatives in multi-herbivore grazing systems (Fig. 3.2).

Camelids have been suggested as good candidates for trophic rewilding (Root-Bernstein and Svenning 2016), defined as the reintroduction of species to restore top-down trophic interactions and trophic cascades to promote self-regulating biodiverse ecosystems (Svenning et al. 2016). This is an emerging ecological restoration strategy that aims to restore ecosystem processes and functions rather than species or populations per se. Although rewilding is increasingly applied as a conservation strategy, especially in developed countries, more empirical research is still needed across a wide range of species and environments (Svenning et al. 2016). As already mentioned, the guanaco can live in extremely arid conditions and take advantage of pastures of low nutritional quality (Schmidt-Nielsen et al. 1957; San Martín and Bryant 1988; Dittmann et al. 2014). Its territorial behavior seems to promote moderate and homogeneous grazing resulting from the balance between population density and forage availability, which would allow restoring the herbivory process in degraded sites (Marino et al. 2016). In this sense, their particular defecation patterns that result in large mounds (latrines) may play a key role in nutrient recycling and vegetation regeneration (Root-Bernstein and Svenning 2016). These characteristics could favor the guanaco's role as a restorer of arid ecosystems. Spontaneous wildlife comebacks increasingly reported worldwide are valuable but still underused sources of ecological information (Svenning et al. 2016). In this sense, the apparent process of passive recolonization of abandoned grazing areas by some guanaco populations in central and southern Patagonia could be an opportunity to develop long-term research programs to evaluate these relevant ecological issues. Finally, climate projections for the coming decades, which predict substantial changes in the frequency and intensity of precipitation and a deepening of desertification processes (IPCC 2021), raise new questions about the response and adaptation capacity of species, particularly herbivores in desert environments, whose food source depends directly on highly variable precipitation pulses (Schwinning and Sala 2004). At the same time, projected climate change scenarios challenge the sustainability of traditional production systems based on single-species grazing. Future research aiming to move toward mixed grazing production schemes in Patagonian rangelands should also focus on assessing the spatiotemporal dynamics of the guanaco–livestock–rangeland relationship in order to predict herbivore responses to different scenarios of long-term global change.

3.5 Future Directions Toward Guanaco–Livestock Coexistence

Human-wildlife conflicts, such as those occurring between livestock production and guanaco conservation, pose complex socio-ecological challenges (Ostrom 2007; Pozo et al. 2021). The outcome of this revision stresses the lack of evidence to support the biological bases of the guanaco–livestock conflict, reinforcing the need to address the human dimensions of the problem to guide management efforts. Social aspects, such as people's perceptions, beliefs, values, and attitudes toward the wildlife they interact with, are relevant to understanding the origins of the conflict and the potential for social change, and hence, to identify effective and viable interventions (Berkes et al. 2000; Hruska et al. 2017). In particular, underlying social drivers of guanaco–livestock conflict in Patagonian rangelands are poorly understood and deserve more research. Proposed frameworks that allow socioeconomic science to be integrated with ecological modeling (e.g., Williamson et al. 2018) could be useful in addressing these seemingly intractable issues.

The problem between the interests of livestock production and guanaco conservation is likely to continue to grow in the future. In order to reduce the tension among the different sectors and promote sustainable range management, we identify three key starting points that should be addressed. First, it is essential to actively discourage the use and dissemination of unfounded ecological arguments that reaffirm distorted ideas regarding guanacos' role in both environmental and husbandry crises. Second, it is also imperative to implement policies and reorient government subsidies to promote the incorporation of available technologies and the development of new management tools oriented to reduce domestic grazing heterogeneity and overstock, thereby improving livestock performance and range condition. Lastly, the current situation requires the development of the technical basis for a genuine sustainable use of guanaco populations, namely, a real productive alternative or complement to livestock production instead of that of a usable resource to self-finance its unjustified culling.

Planning, design, and implementation of management schemes affecting guanaco populations require strengthening participatory processes involving all relevant stakeholders (i.e., ranchers, pastoralists, indigenous peoples, scientists, conservationists, and policymakers). Such schemes should have an adaptive management approach of knowledge co-production, including transparent co-participation in the follow-up and monitoring of processes, as well as the horizontal transmission of management results among stakeholders. Knowledge co-production has been identified as one of the essential processes for effective applications of ecological research in management actions (Wisdom et al. 2020). Government agencies should promote this cooperation through programs that strengthen their institutional capacities for wildlife and livestock management. In summary, we argue that moving toward a guanaco–livestock coexistence scenario for Patagonian rangelands will require building participatory solutions on a sound ecological evidence base, incorporating in-depth knowledge of the social drivers of the conflict in a framework of transdisciplinary programs with a strong long-term institutional commitment.

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Chapter 4
Health Risks for Guanaco (*Lama guanicoe*) Conservation

Virginia Rago, Carolina Marull, Hebe Ferreyra, Pablo Carmanchahi, and Marcela Uhart

4.1 Introduction

Wild animals naturally coexist with a variety of host-adapted biological agents that exert regulatory forces on their populations (Beldoménico 2006). In this context and in an undisturbed natural environment, the occurrence of disease is rarely a threat to

V. Rago (✉)
Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCo), Junín de los Andes, Neuquén, Argentina
e-mail: virginiarago@comahue-conicet.gob.ar

C. Marull
Reserva Natural Urbana Quilque Lil, Aluminé, Argentina
e-mail: carolinamarull@gmail.com

H. Ferreyra
Cátedra de Fauna Silvestre, Universidad Nacional de Villa María, Córdoba, Argentina
e-mail: hvferreyra@unvm.edu.ar

P. Carmanchahi
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCo), San Martín de los Andes, Neuquén, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina
e-mail: pablocarman@comahue-conicet.gob.ar

M. Uhart
One Health Institute, School of Veterinary Medicine, University of California, Davis, CA, USA
e-mail: muhart@ucdavis.edu

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_4

species conservation, but rather acts as a factor of natural selection (Beldoménico 2006). However, the complex relationship between pathogens and wild species can be altered by human activity. The pathways by which disease risks increase are variable and generally result from multiple factors, which underlie and converge to trigger and/or enhance their occurrence (Aguirre and Tabor 2008). Changes in land use, the introduction of alien species, overexploitation of natural resources, and unusual weather conditions, among others, can alter natural ecosystems and are associated with reduced habitat quality, detriment to the health of wild animals, and increased disease transmission (Acevedo-Whitehouse and Duffus 2009; Gottdenker et al. 2014).

Areas where wild species, domestic species, and human activity overlap create interface scenarios where pathogens can cross species barriers. The impact of species jumps, called spillover, will depend on numerous factors associated with the pathogen (virulence, specificity, etc.), the host (immunity, general condition, etc.), and the environment (temperature, humidity, etc.). Stress plays a key role in the interaction between the host and the potentially pathogenic agent, weakening the physiological and immunological condition of the host. This may predispose to infections, further worsening host health (Beldoménico and Begon 2010). Wild animals that share environments with livestock manifest increases in cortisol metabolites, the main hormone indicator of stress, as has been reported in Apennine chamois (*Rupicapra pyrenaica ornata*) (Formenti et al. 2018). Studies in La Payunia Provincial Reserve (Mendoza province, Argentina) have shown spatial segregation and competitive interactions between guanacos and small livestock throughout the year (Schroeder et al. 2013, see Chap. 2). This competitive situation is exacerbated by natural factors such as droughts, which can have a severe impact on the population dynamics of herbivores that inhabit arid and semi-arid environments (Duncan et al. 2012). Water scarcity can force wildlife species to share water sources with livestock that increase opportunities for disease transmission. This was observed in La Payunia Reserve, where there are only a few springs with reduced flows and temporary wells with water accumulation from scarce rainfall (Candia et al. 1993). At this site, the available water is used by both livestock and wildlife, including guanacos. Because most of Patagonia has a marked water deficit (Paruelo et al. 2000), situations of extreme drought, food competition with sheep, limited dispersal of guanaco due to the presence of fences or livestock (Baldi et al. 2001; Rey et al. 2012; Antún and Baldi 2020), and extreme climatic conditions have triggered mass mortalities of guanacos.

Poaching is another important stress factor for guanacos. It has been shown that guanacos avoid areas where hunting pressure is high, thus limiting their grazing areas and consequently impacting their energy reserves and survival (Donadio and Buskirk 2006). Fragmentation of wild populations can affect disease dynamics, as loss of connectivity between populations reduces genetic diversity, which can lead to low fitness of individuals (De Bois et al. 1990; Poirier et al. 2019), reduced ability to cope, adapt, and survive environmental changes (Soler 1998; Castro et al. 2011) and increased vulnerability to disease (Lyles and Dobson 1993). Exposure to pathogens in wild animals can result in a range of outcomes, from asymptomatic infections to severe infections, including death (Nettleton 1990; Celedón et al. 2001; Bengis 2002). In some cases, wild species may become reservoirs of disease. Such is the case of paratuberculosis (or Johne's disease) from cattle, caused by *Mycobacterium avium paratuberculosis* (MAP) that causes asymptomatic infection in wild animals, yet they can contribute to the maintenance of the infection (Florou et al. 2008). Various livestock pathogens cause disease in wild ungulates (Meagher and Meyer 1994; Giacometti et al. 2002; Besser et al. 2017). For example, in Chile, huemul (*Hippocamelus bisulcus*), an endemic and endangered cervid, is severely affected by caseous lymphadenitis, a chronic bacterial disease caused by *Corynebacterium pseudotuberculosis* of sheep (Morales et al. 2017) and by a paramyxovirus with a high genetic identity with bovine papular stomatitis virus and bovine pseudopoxvirus causing severe foot disease (Vila et al. 2019). Similar scenarios have been reported with some parasites. For example, sarcoptic mange caused by the mite *Sarcoptes scabiei*, with probable origin in cattle, has affected wild ungulates in Europe (León-Vizcaíno et al. 1999; Moroni et al. 2021).

This chapter reviews the state of knowledge of diseases that affect or could have a negative impact on the health of wild guanaco populations in Patagonia, compiling both published data and information from various gray literature sources such as technical reports and reports for government agencies. In addition, unpublished data from the authors are included, analyzing those pathogens that are potentially risky and to which further attention should be paid. This chapter also discusses the need for systematic health monitoring to allow early detection of diseases and predisposing factors that may be affecting the fitness and health of wildlife overall. In this sense, activities where guanacos are handled (e.g., management for shearing of wild guanacos) provide an excellent opportunity for health assessments.

4.2 Current Knowledge of Diseases of Free-Ranging Guanaco in Patagonia

The detection of potential pathogens and the occurrence of diseases in free-ranging guanacos is an area little addressed to date. Particularly for Patagonian guanacos, few studies have focused on wild populations. Here, we summarize the main findings of studies by other researchers and our own, referencing information from captive guanacos and domestic camelids.

4.2.1 Parasitic Diseases

4.2.1.1 Endoparasites

Many endoparasite species only need to contaminate pastures with infesting larvae for transmission (Walker and Morgan 2014). This group of pathogens is the most studied and reported agents in wild guanacos due to their ease of detection and potential transmission with sheep and cattle (Navone and Merino 1989). Recently, a review by González-Rivas et al. (2019) mentioned the presence of 14 genera and 26 species of parasites for guanacos in Argentina, with a higher abundance of species of the *Phylum* Nematoda, followed by Aplicomplexa and Platyhelminthes, and a marked richness in wild guanacos from the Patagonian steppe compared to populations from the Patagonian Andean forest or the puna. In the transition zone between the Patagonian steppe and the monte ecoregion, in central western Argentina, Moreno et al. (2015) identified by light microscopy five species of gastrointestinal nematodes in wild guanaco feces, of which two *Nematodirus* spp., one *Strongyloides* sp. and *Moniezia benedeni*, are considered typical of domestic ruminants. These findings were not associated by the authors with physical deterioration of infested guanacos.

In wild guanacos that massively died in Protected Area Cabo Dos Bahías (Chubut province, Argentina), in the Patagonian steppe, the finding of high loads of *Dictyocaulus filaria* nematodes in bronchi was associated with lung damage in individuals weakened by starvation (Beldoménico et al. 2003). In addition, the presence of *Moniezia expansa*, a common parasite of sheep, was documented in this study. These findings suggested that, under certain circumstances, such as extreme climatic conditions and poor forage quality, parasites can act as a morbidity and mortality factor for guanacos (Beldoménico et al. 2003; see Box 4.1).

Box 4.1: Massive Mortality of Wild Guanacos in Protected Area Cabo Dos Bahías

In winter (June/July) 2000, an estimated 70–90% of the population (approximately 323 individuals) of wild guanacos living in the Cabo Dos Bahías, Chubut province, died. Prior to the event, the protected area was in a serious state of degradation with an absence of palatable plant species, the presence of sheep from neighboring farms, a marked drought from the previous year, and a high density of guanacos within the area (40 guanacos per km^2, Baldi et al. 2001).

In early August 2000, a team of biologists and veterinarians joined efforts to investigate the event. Twelve dead guanacos were necropsied, and a thorough investigation was conducted, including histopathology, parasitology, and analysis of rumen contents for dietary analysis to determine the cause of death. Most of the dead animals were found in family groups, the calves close to their mothers, and in almost all cases, the animals were in the shelter of a bush or rocky outcrop.

(continued)

Box 4.1 (continued)

Macroscopically, the guanacos examined were in very poor body condition, with an absence of fat reserves and reduced muscle mass. Adult females were not pregnant despite being a trimester away from the calving season. Histopathological results found no evidence of lesions of infectious origin. However, severe autolysis, present in all samples, could have masked some lesions. Parasitological studies revealed high parasite loads, some of them pathogenic and frequent in sheep (Beldoménico et al. 2003). The rumen contents analyzed showed ingestion of vegetation of null nutritional value. These findings supported the hypothesis that death was caused by chronic malnutrition and severe starvation, in most cases coupled with lung congestion and high burdens of lung parasites.

Parasites such as *Lamanema chavezi* and *Sarcocystis* spp. have severe implications for the extractive use of wild guanacos, generating great economic losses due to the confiscation of viscera and meat at abbatoirs. The presence of lesions and cysts in the liver and muscle that affect the appearance of consumable parts leads to their rejection and discard, thus unjustifying slaughter (Skewes et al. 2000; see Chap. 6). *L. chavezi* (family: Molineidae) causes gastroenteritis and verminous hepatitis in domestic South American camelids (Jarvinen et al. 2014). Santana et al. (2020) conducted a study during the harvest of wild guanaco in Santa Cruz province in 2017–2018 (MAyDS Resolución No 766-E/17), where they reported this parasite for the first time in the area, associated with macroscopic liver damage. Although according to the authors affected guanaco showed no signs of disease or evident physical deterioration, in domestic camelids such as the llama (*Lama glama*) this parasite has caused lethargy, decay, weight loss, and even death (Jarvinen et al. 2014).

Sarcocystis spp. (Apicomplexa) have indirect life cycles where canids and felids serve as main definitive hosts while a range of domestic and wild animals serve as intermediate hosts, including South American camelids such as alpacas, llamas, and guanacos (Saeed et al. 2018). *Sarcocystis* spp. infections are mostly asymptomatic in South American camelids (Schnake et al. 2016), but significant lesions can be observed in affected tissues (Gabor et al. 2010). *S. mansoni* and *S. aucheniae* develop microscopic or macroscopic cysts, respectively, primarily in skeletal muscles of the tongue, neck, diaphragm, and legs and in cardiac muscle (Saeed et al. 2018; Moré et al. 2016). During the 2017–2018 wild guanaco harvest in Santa Cruz province, lesions compatible with *Sarcocystis* spp. were detected in up to 77% of the carcasses examined in two farms (total carcasses examined, $n = 2042$; Final Report. Proyecto Estratégico Uso Integral y Sustentable del Guanaco Silvestre. 2019). A similar prevalence was reported in harvested guanaco in Tierra del Fuego, Chile (Skewes et al. 2000).

Another parasite that causes viscera confiscations in harvested guanacos is the larval stage of *Echinococcus granulosus*, which causes hydatid cysts in the affected tissues (Leguía and Casas 1999; SAG 2015; Swanhouse S.A. 2016). *E. granulosus* is a zoonotic pathogen that causes serious disease in humans (Acha and Szyfres 2003). The cycle involves carnivores acting as definitive hosts, shedding the infective forms into the environment in their feces, and herbivores act as intermediate hosts, generating cysts in tissues such as the lung and liver, which are then consumed by carnivores to continue the cycle (Soulsby 1988). Sheep are considered the most important host for hydatid disease because of their high infection rate, fertility of cysts (90%), and close relationship with dogs (Soulsby 1988). There are documented wild cycles in various parts of the world, such as in Alaska and Canada, where it was detected in wild carnivores, with the highest prevalence in wolves (*Canis lupus*) and coyotes (*Canis latrans*) (Schurer et al. 2018), in Australia between dingoes (*Canis lupus dingo*) and marsupials (Jenkins 2021), and in Chile between grey fox (*Pseudalopex griseus*) and sheep (Aguilera 2001). Permanent monitoring of this parasite is important given its zoonotic characteristics; however, available information refers to a low prevalence in wild guanacos. For example, in guanaco harvests carried out in the Chilean portion of Tierra del Fuego Island, prevalence of 0% (Valdevenito 2008) to 3.1% were reported (Cunazza 1985; Swanhouse S.A. 2016).

Finally, antibodies to the protozoan *Toxoplasma gondii* (Apicomplexa) have been reported in guanacos from Mendoza, Neuquén, and Rio Negro provinces (Marull et al. 2012) (Table 4.1). *T. gondii* circulates in wild and domestic ungulates with higher prevalence in areas where species overlap (Dubey 2010; Almería et al. 2021). In domestic camelids, Ramirez et al. (2005) detected moderate to high seroprevalences in alpacas (*Lama pacos*) sharing habitats with small domestic ruminants. Although *T. gondii* causes abortions and deaths in sheep and goats (Acha and Szyfres 2003; Ramirez et al. 2005), the finding of apparently healthy wild guanacos with antibodies suggests that asymptomatic or subclinical infections may occur. The impact on the health of guanacos is currently unknown, but disease presentations and mortality depend on the susceptibility of the species, host–parasite relationship, and immune response (Juan-Sallés et al. 2011).

4.2.1.2 Ectoparasites

Among ectoparasites, sarcoptic mange, caused by the mite *Sarcoptes scabiei*, is undoubtedly the most relevant for South American camelids at present (Bujaico and Zuñiga 2016; Beltrán-Saavedra et al. 2011; Ferreyra et al. 2022). *S. scabiei* induces skin hypersensitivity, inflammation, intense itching, pain, and hair loss (Bornstein et al. 2001; Pence and Ueckermann 2002). As the disease progresses, the skin thickens and develops deep fissures, impairing thermoregulation, progressive emaciation, and limited ability to forage and evade predators (Carvalho et al. 2015; Simpson et al. 2016). Sarcoptic mange is a common infestation in llamas and alpacas (Bornstein and de Verdier 2010), and although there are no prevalence studies and few published data on sarcoptic mange in llamas from Argentina, outbreaks have been detected in the north of the country in captivity (Aráoz et al. 2016), and in free-ranging herds (pers. observ., Ferreyra Hebe). This disease has also been reported in

Table 4.1 Positive seroprevalence found in wild guanacos from Río Negro, Neuquén, and Mendoza provinces

Year	Province	*n*	BSV	IBR	ROT	PI-3	LEP	TOX
2004	Río Negro	36	NT	3/32 (9%)	NT	3/30 (10%)	9/36 (25%)	1/25 (4%)
2005	Rio Negro	18	NT	1/18 (5%)	NT	2/16 (12%)	1/15 (6%)	NT
2001	Neuquén	26	NT	17/19 (89%)	NT	20/20 (100%)	19/19 (100%)	2/26 (7%)
2002	Neuquén	24	NT	18/24 (75%)	NT	21/24 (87%)	17/24 (70%)	5/12 (41%)
2004	Neuquén	18	NT	5/18 (27%)	NT	15/18 (83%)	14/17 (82%)	3/17 (17%)
2005	Mendoza	14	NT	4/14 (28%)	NT	5/12 (41%)	0/14 (0%)	0/12 (0%)
2006	Mendoza	68	1/65 (1.5%)	3/65 (4%)	57/65 (87%)	41/65 (63%)	0/65 (0%)	11/55 (20%)
2007	Mendoza	65	NT	0/65 (0%)	NT	47/58 (81%)	21/58 (36%)	11/47 (23%)
2009	Mendoza	52	NT	0/52 (0%)	52/52 (100%)	40/52 (77%)	8/52 (15%)	NT
2010	Mendoza	35	NT	0/35 (0%)	30/34 (88%)	NT	NT	NT

Positive/total tested (Seroprevalence): *NT* not tested, *BSV* bovine respiratory syncytial virus, *IBR* infectious bovine rhinotracheitis, *LEP Leptospira* spp., *PI-3* parainflueza-3 virus, *ROT* rotavirus, *TOX Toxoplasma* sp. Diagnostic methods: **ROT** enzyme-linked immunosorbent assay (ELISA), **PI-3** hemagglutination inhibition test (IHA), **IBR** serum neutralization test, ***Toxoplasma* sp**. IHA, **BSV** ELISA, and **LEP** microscopic agglutination test wild South American camelids. In vicuña, the prevalence appears to be low in some areas such as the Puna ecoregion of Jujuy province in Argentina (Arzamendia et al. 2012). In 2014 an outbreak of sarcoptic mange was first detected in vicuñas and guanacos in San Guillermo National Park (northwest of Patagonia). Over the next two years, vicuña populations declined by 55 and 98%, and guanaco declined by ~95% (Ferreyra et al. 2020). Later between 2017–2018, the population continued to crash, with further reductions in vicuñas and guanaco densities (68% and 98%, respectively). By April 2019 no vicuñas or guanacos were found at the study site, suggesting their near extinction in the park (Ferreyra et al. 2022). The guanaco and vicuña mites recovered during the outbreak presented highly homologous genotypes, being mostly monomorphic in all loci and most of them sharing the same alleles with very little genetic variability. This is consistent with a single and recent origin of the epidemic, supporting the hypothesis that the outbreak originated from mangy llamas introduced from northern Argentina during a livestock incentive program (Ferreyra et al. 2022). In Chile, Montecino et al. (2019) reported that abnormally alopecic wild mammals (a proxy for mange) seem to have become more common since 2004, with South American camelids being the second most affected taxa. Likewise, a prevalence of 33% for sarcoptic mange has been reported in guanacos harvested in Tierra del Fuego, Chile (Alvarado 2004). Notwithstanding, about 800 km south of San Juan province, in La Payunia Reserve (Mendoza province), between 2005 and 2016, 1241 wild guanacos sheared and clinically checked by veterinarians, the authors of this chapter, did not present skin lesions (Carmanchahi, 2005–2016, Shearing management reports). The same was observed in one farm in Río Negro province, between 2005 and 2008 (n = 2934; Carmanchahi 2005–2008, Shearing management reports) and in two private farms in Neuquén province, where 64 wild guanacos were evaluated (Carmanchahi 2004, Shearing management report).

4.2.2 Viral and Bacterial Diseases

Serological tests that detect specific antibodies against different pathogens are one of the most commonly used methods to assess exposure to relevant viruses and bacteria in wildlife populations (Gilbert et al. 2013). One limitation, however, is that not all methods used for wildlife have been validated in nondomestic species (Gilbert et al. 2013; OIE 2018). To date, only two seroprevalence studies reporting the proportion of individuals within a population with pathogen-specific antibodies in their serum have been conducted in wild guanacos in Argentina (Karesh et al. 1998; Marull et al. 2012). There are some reports in captive guanacos (Parreño et al. 2001, 2004; Llorente et al. 2002, among others).

Marull et al. (2012) studied wild guanacos from the provinces of Mendoza (2005–2007, 2009 and 2010), Río Negro (2004 and 2005), and Neuquén (2001, 2002, and 2004) handled for live-shearing during the prepartum season (spring). Karesh et al. (1998) studied 20 wild guanacos from Chubut province in the postpartum season (summer). Both studies reported that guanacos sampled were in good condition and without signs of disease. Karesh et al. (1998) reported negative serological results for 11 pathogens: bluetongue virus, bovine viral diarrhea, equine herpesvirus-1, infectious bovine rhinotracheitis, *Leptospira* sp., *Brucella mellitensis*, *M. paratuberculosis*, bovine respiratory syncytial virus, parainflueza-3, foot and mouth disease, and vesicular stomatitis. In the study by Marull et al. (2012), antibodies were detected for 6 of the 12 diseases tested (Table 4.1). No antibodies were detected for bovine viral diarrhea, foot and mouth disease, bluetongue virus, enzootic bovine leukosis, *Brucella* sp., and *Mycobacterium paratuberculosis* (not included in Table 4.1).

In relation to the findings reported in Table 4.1 rotavirus (ROT) presented high seroprevalence in the three years tested. ROT is an enteric virus that affects both domestic and wild ungulates, particularly calves, causing watery diarrhea and intestinal lesions (Kapil et al. 2009). Parreño et al. (2001, 2004) reported rotavirus mortality in newborn captive guanacos in two farms from Río Negro and Chubut provinces (in close contact with cattle). They isolated the virus and recorded a high seroprevalence in recovered individuals. The high seroprevalence observed in adult wild guanaco populations in Mendoza province could reflect past infections in offspring. It is not known whether detected antibodies come from a source external to the guanaco population.

Parainfluenza-3 virus had a high seroprevalence in Neuquén and Mendoza provinces. This virus causes respiratory disease in cattle, and although it does not appear to be of relevance to the health of guanacos in the populations sampled, the virus has been isolated from a juvenile guanaco that died of acute respiratory disease in Chile (Vergara Proboste 2004), although the author does not specify whether it was a wild or captive individual.

Seroprevalence to infectious bovine rhinotracheitis was low in Río Negro and Mendoza, but high in Neuquén. This disease is caused by bovine herpesvirus-1, a pathogen primarily of cattle that causes an upper respiratory infection, viral pneumonia, reproductive tract infections (vaginitis and balanoposthitis), keratoconjunctivitis, encephalitis, and abortions (Williams and Barker 2008). The role of bovine herpesvirus in causing disease in South American camelids is not established (Celedón et al. 2001).

In Marull et al. (2012), the seroprevalence for bovine respiratory syncytial virus was very low (1.5%), although because serology was limited in time and space, its interpretation should be taken with caution. To the best of our knowledge, there are no previous reports of antibodies to this pathogen in South American camelids.

For *Leptospira* sp., the serovars for which antibodies were identified were *copenhageni* (serogroup *Icterohaemorrhagiae*), *pomona* (serogroup *Pomona*), and *castellonis* (serogroup *Ballum*), and the highest seroprevalences were detected in Neuquén (Marull et al. 2012). Llorente et al. (2002) reported antibodies to serovars *wolffi* (*Sejroe* serogroup) and *copenhageni* (*Icterohaemorrhagiae* serogroup) in captive guanacos from Río Negro. Leptospirosis is an endemic bacterial disease in Argentina, with occasional epidemic outbreaks in livestock and a high impact on reproduction due to abortions, perinatal mortality, or births of weak or infertile individuals. It has a complex epidemiology and cosmopolitan distribution. Several species, mainly rodents, act as reservoirs for many serovars, with humans and animals being accidental hosts (Brihuega et al. 2017).

The studies described here were based on serology rather than the detection of pathogens. The interpretation of the results should not overlook limitations inherent to the study of antibodies in wild animals, such as that the antibodies detected do not indicate current infection, that in offspring the antibodies found may be of maternal origin rather than direct exposure to the pathogen, that there may be differences between laboratories for the same pathogen, that there are tests that have not been validated in wildlife, that there may be cross-reactivity of antibodies to multiple pathogens so that they can be positive to one or another with similar antigenic reaction, and that a negative result does not mean the animal was not exposed to that pathogen as some antibodies are short-lived, among several other considerations (Gilbert et al. 2013). However, serological studies are very useful for longitudinal or cross-sectional sampling studies to collect data on the incidence and prevalence of a pathogen and to infer the dynamics of temporal or spatial infection in wildlife populations. Longitudinal studies repeat the sampling of individuals, social groups, or populations to detect changes in the prevalence of antibodies over time and can be used to estimate the incidence of infection if the sample size is large enough to detect events of seroconversion of antibodies in the population (Gilbert et al. 2013).

4.2.3 Other Pathogens to Consider for Health Monitoring of Guanaco Populations

The two existing studies (Karesh et al. 1998; Marull et al. 2012) reported negative seroprevalence for nine pathogens. However, due to their potential impact on the health of guanacos and implications at the livestock or human interface, some of these pathogens should be considered for monitoring and surveillance of these populations.

Mycobacterium avium paratuberculosis (MAP) is a bacterial pathogen of domestic animals and was isolated from the fecal material of wild guanacos from Chile (Tierra del Fuego) with low prevalence (4.2%, 21/501), and, in all cases, was characterized as the cattle-type strain (Salgado et al. 2009). The authors made no comments about the clinical condition of these guanacos. MAP is the causative agent of contagious, chronic, and typically fatal enteric disease of domestic and nondomestic ruminants (Carta et al. 2013). Clinically affected animals present wasting and emaciation. However, MAP can also infect non-ruminant animal species with less specific signs (Roller et al. 2020). Recently, Corti et al. (2021) showed that the prevalence of infection is higher in wild guanacos sharing habitats with sheep suggesting that sheep populations may be the main source of infection for susceptible animals due to their large numbers, which drive MAP dynamics.

Brucella sp. is a bacterium that causes reproductive disease in animals, and to the best of our knowledge, there are no reports of infection in guanacos. Although it is not a major disease of camelids, it is relevant because of its zoonotic potential. Bardenstein et al. (2021) described an outbreak in humans associated with the consumption of commercially sold camel milk containing *Brucella melitensis* in Israel. *B. mellitensis* is primarily pathogenic in goats and sheep, so its study in wild guanacos cohabiting with small livestock should be encouraged. *B. abortus* infection (including abortion) has been produced experimentally in llamas, but no natural cases have been reported in South American camelids (Kapil et al. 2009).

Equine herpesvirus type 1 was only studied by serology in Cabo Dos Bahias in Chubut province (Karesh et al. 1998) with negative results. It is a globally distributed pathogen that affects all equids causing abortions and neonatal deaths, respiratory disease, and neurological disorders (Dunowska 2018). Blindness in alpacas and llamas from Chile were attributed to infection to equine herpesvirus infection (Kapil et al. 2009). Vergara Proboste (2004) reported positive serology in South American camelids, including wild guanacos in Chile (IV and XII Regions), concluding that in Chile there are South American camelids infected with this virus or a herpesvirus that shares common antigens. To date, there is no information on the relevance of this virus for South American camelids. However, it should be considered in areas where guanacos cohabit with large herds of feral horses, like in Parque Nacional Patagonia, Santa Cruz province, Argentina (Roesler and Fasola 2020).

Some pathogens such as the contagious ecthyma virus, which affects domestic ungulates, have not been evaluated in wild guanacos. This is a globally distributed, highly contagious viral disease that affects the skin and mucous membranes of sheep and goats (Robles et al. 2017). There are reports that this disease affects wild ungulates such as wapiti (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*) and it is also zoonotic (Samuel et al. 1975; Lance et al. 1983). In Argentinean Patagonia, contagious ecthyma is widely spread in sheep and goats causing epidemic outbreaks on a seasonal basis (spring/summer) with loss of body condition in affected animals (Robles and Olaechea 2001). In domestic camelids, typical proliferative lesions have been documented in the epidermis of the mouth commissures, which can extend to the rest of the face and perineum and can evolve into a more chronic course than in sheep, and also affect areas of the skin in a similar way to sarcoptic mange (Fowler 1998). In Peru, seropositivity was detected in alpacas with lesions (Kapil et al. 2009).

4.3 Why Monitor Guanaco Health?

Information on the health of wild guanaco populations is very scarce despite them being a key species in arid and semi-arid Patagonian ecosystems due to their role as prey of the largest native carnivore, the puma, and main consumer of plant species. To fill this void, health studies of guanacos should be encouraged, particularly as populations are increasingly managed and subject to use (e.g., live-shearing, harvest). Disease surveillance can be carried out opportunistically and via different methods, such as serological monitoring of pathogen exposure when animals are handled, to noninvasive studies by fecal sampling. In addition, efforts should be increased for the investigation of morbidity and mortality events, including pathogen detection and pathological examination. Particularly in harvested populations, access to carcasses for health research should be a prime goal. Health monitoring would enable risk-mapping and identifying areas of particular concern, as well as guide management actions for the species and its habitat. In this sense, the health status of sympatric livestock is of particular relevance. Notably, contrary to wildlife, livestock diseases can be controlled via husbandry, vaccination, and deworming. It is also easier to detect and investigate outbreaks of transmissible diseases in domestic animals.

Considering the limited studies available to date, it appears that parasites are more relevant in wild guanacos than viral or bacterial agents. However, it is possible that the bias toward the more frequent diagnosis of parasitic forms is related to the greater ease of their study and the possibility of noninvasive access to samples (e.g., feces). The effects of parasitic diseases are generally less visible, stemming from a lower feed conversion efficiency, weight loss, gastrointestinal disorders, anemic states, etc. (Cáceres 2000). In wild guanacos, these effects can be very difficult to measure if the parasite study is not associated with population and environmental studies, such as the presence of livestock or other alien species and climatic factors, among others.

Sarcoptic mange merits special attention at this time, particularly in guanaco populations within protected areas. Sarcoptic mange is a highly contagious and expanding disease of wild animals, both geographically and in terms of host species, and is therefore considered an emerging disease (Escobar et al. 2021). In protected areas and populations under management, mange outbreaks should be quickly addressed, and interventions to control the outbreak at the onset must be considered. Adequate investigation of mange outbreaks should aim to identify the source and origin of infestations, mite host preference, mechanisms of spread, etc. (Arlian and Morgan 2017; Escobar et al. 2021; Moroni et al. 2021). Although guanacos with lesions compatible with mange have been observed in the Patagonian steppe in Argentina (e.g., Protected Area Cabo Dos Bahías in Chubut province, Uhart M. pers. observ.), the distribution, prevalence, and impact on guanaco populations are unknown. Mange also has implications for fiber shearing and should thus be monitored closely in populations subject to management and use (Papadopoulos and Fthenakis 2012).

In the case of guanacos slaughtered for consumption, the high prevalence of sarcosporidia results in the discarding of large portions of potentially edible meat. This results in unnecessary guanaco deaths as it is impossible to know in advance the load of parasitic cysts or lesions in body tissues at the time of harvest. Studies to establish geographical areas with a lower prevalence of the parasite in guanacos are essential for the sustainable use of this resource under a lethal extraction model. Moreover, in areas with high *Sarcocystis* sp. loads, only management for nonlethal fiber extraction (live shearing, see Chap. 6) should be authorized. Such mapping of the use of the species must be accompanied by interdisciplinary scientific research and supporting regulations.

Morbidity and mortality events in wild guanacos must be addressed at the time of their occurrence and in a multidisciplinary manner in order to reach conclusions that are useful for the study and conservation of the species. In this sense, should a mortality event occur, it is important to complement the health investigation with information on the historical and current livestock stocking rates in the surrounding areas, soil conditions (e.g., desertification), health and husbandry of livestock, and presence or introduction of livestock or alien species, among others. To the best of our knowledge, past mortality events have rarely been comprehensively investigated. The cause of death was investigated in guanacos that died in Protected Area Cabo dos Bahías (Chubut province, Baldi et al. 2001, see Box 4.1) and in San Guillermo National Park (San Juan province, Ferreyra et al. 2022). But in other massive mortality events that occurred in Santa Cruz province in 2006 (Rindel and Belardi 2006) and more recently during 2020 (La Opinión Austral 2020), no health studies of the dead individuals or the remaining population were carried out.

Disease control in wild animals is complex and most often unfeasible. Consideration of possible interventions must be based on a sound knowledge of the biology of the pathogen and the affected species, as well as the ecology of the affected population (Wobeser 2002). For these reasons, increased monitoring, detection, and diagnostic efforts, as well as analysis of the ecological context, are essential for the prevention of wildlife diseases. Health is the capacity of animals to respond to and overcome change (Ryser-Degiorgis 2013). It is likely that conditions will become increasingly averse for guanacos (and other wildlife) and that maintaining physiological homeostasis will in turn become increasingly challenging for these species. Concerted efforts to sustain healthy, resilient guanaco populations will be essential for the successful conservation of Patagonia biodiversity.

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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, and William L. Franklin

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),

E. Donadio (✉)
Fundación Rewilding Argentina, Buenos Aires, Argentina
e-mail: edonadio@rewildingargentina.org

J. I. Zanón Martínez
Instituto de Ciencias de la Tierra y Ambientales de La Pampa, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina
e-mail: jzanon@conicet.gob.ar

P. Alarcón
Conservación Patagónica Asociación Civil, San Carlos de Bariloche, Argentina
e-mail: pabloalarcon@comahue-conicet.gob.ar

W. L. Franklin
Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA, USA

IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina
e-mail: wlf@myomnitel.com

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_5

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 km^2 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, Argentina[1–3]; Bosques Petrificados, Perito Moreno, and Monte Leon national parks[4–5]; 25 de Marzo and Doraike ranches

		Major food categories				
		Native		Exotic		
Region/protection	References	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/km^2) 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 km^2 (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 km^2 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

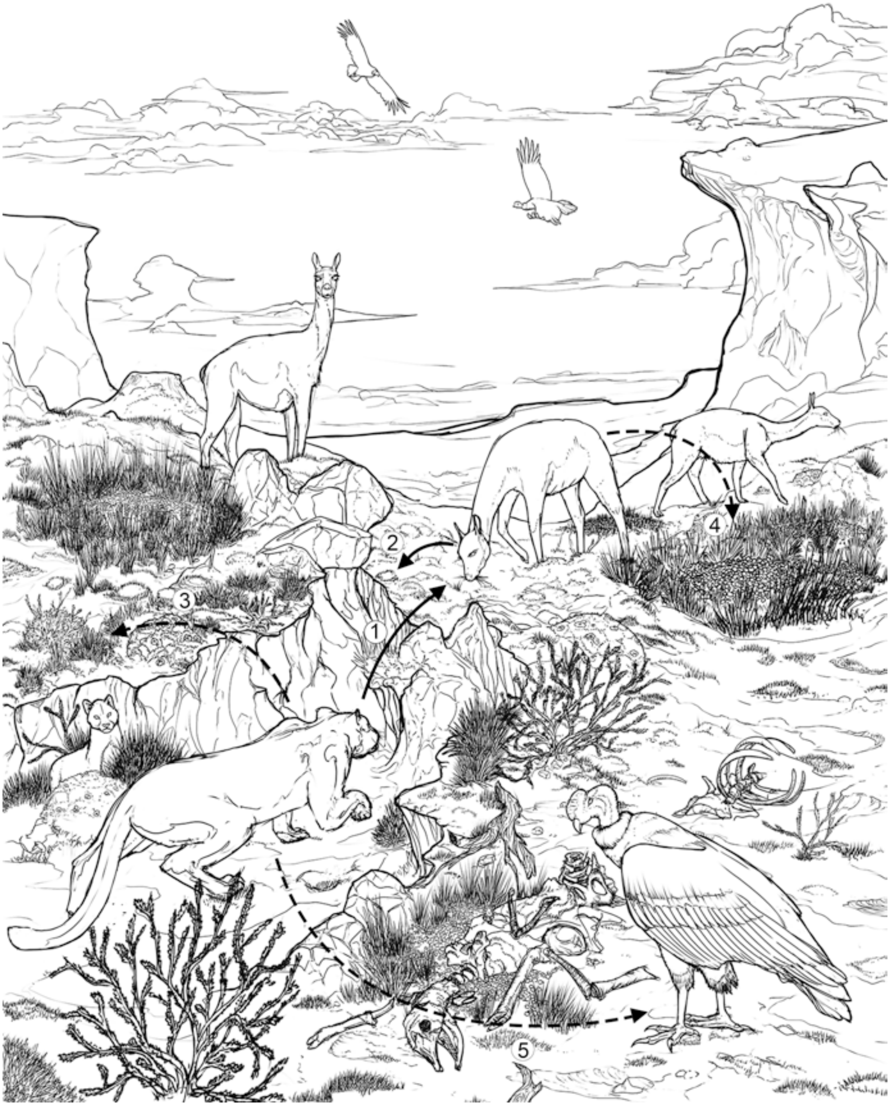

Fig. 5.1 Conceptual model depicting some of the community and ecosystem-level effects of a hypothesized trophic cascade triggered by the guanaco–puma dyad. Solid lines show direct negative interactions. Broken lines show indirect positive interactions. Puma predation on guanacos limits the numbers of 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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Chapter 6
International Policies and National Legislation Concerning Guanaco Conservation, Management and Trade in Argentina and the Drivers That Shaped Them

Gabriela Lichtenstein, Pablo Carmanchahi, Martín Cristian Funes, Román Baigún, and Adrian Schiavini

6.1 Introduction

Sustainable use of wild species does not occur in a vacuum, but in contexts with different institutional arrangements and governance systems, where individuals or groups have different rights, roles, interests, and responsibilities, which are in turn framed by power relationships. Natural resource management is highly complex and characterized by multiple levels of policy implementation; multiple perceptions

G. Lichtenstein (✉)
Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires (UBA), Buenos Aires, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina
e-mail: lichtensteingabriela@gmail.com

P. Carmanchahi
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue, Argentina (UNCO), San Martín de los Andes, Neuquén, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina
e-mail: pablocarman@comahue-conicet.gob.ar

M. C. Funes
IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina

Wildlife Conservation Society, New York, United States of America
e-mail: mfunes@wcs.org

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_6

of the problem and the objectives of policy implementation; multiple strategies and policy instruments for policy implementation (Bellamy2007). This complexity can well be illustrated with the development of conservation and management policies for guanaco in Argentina during the last decades.

In this chapter, we explore changes in international and national public policies in relation to guanaco conservation and management in Argentina from 1993 to the present, and the drivers that influenced them.

This system enables us to analyse the different outlooks on the environment and development, the uneven power relationships among stakeholders, the failure of top-down governmental policies that led to decoupling[1] of the social and ecological systems (see Chap. 9), and the need for coordination and cooperation across the horizontal and vertical dimensions of policy and institutional systems as well as stakeholder participation.

6.2 Guanaco Governance in Argentina

Argentina is a federal country comprising 23 provinces, with legislative powers divided between the federal state and the provinces. Under the Constitutional Reform (1994), the provinces are the original owners of the natural resources within the boundaries of their respective territories and they are exclusively empowered to determine their use. However, the Constitution also enables the federal government to make minimum requirement regimes, which are sets of rules granting, for example, common environmental protection for the national territory and setting the conditions for environmental preservation and sustainable development. International Conventions or Treaties signed by the country (e.g. the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); or the Convention on Biological Diversity (CBD)) hold a higher hierarchy than national laws, paralleling the constitutional level.

[1] As in Chap. 9, we borrow the term "decoupling" from Hoole and Berkes (2010), to mean the separation of the communities from their traditional territory, the "decoupling" or alienation of people from their local environment and their cultural heritage.

R. Baigún
IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina

Wetlands International/Fundación Humedales, Buenos Aires, Argentina
e-mail: rbaigun@humedales.org.ar

A. Schiavini
IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina

Wildlife Conservation Society, New York, United States of America

Centro Austral de Investigaciones Científicas (CADIC – CONICET), Universidad Nacional de Tierra del Fuego, Ushuaia, Antártida e Islas del Atlántico Sur, Argentina
e-mail: aschiavini@gmail.com

The Argentine Civil and Commercial Code declares wildlife *res nullius* (however see Box 6.1). Therefore, the chances of legally appropriating wildlife are higher for citizens with large properties (e.g., ranch owners, those that organize duck, dove or big game hunting or fishing expeditions) than for smallholders and subsistence rural inhabitants (Lichtenstein 2013). In the latter case, appropriation occurs mainly through subsistence hunting (Altricher and Basurto 2008; Funes and Novaro 1999), management in communal areas (e.g. vicuñas Lichtenstein and Cowan Ros 2021), or protected areas (Lichtenstein and Carmanchahi 2012). Many of Argentina's public policies regarding natural resource management reflect the historical denial of

Box 6.1: Who Does Fauna Belong to in Argentina?

Ana Di Pangracio
Fundación Ambiente y Recursos Naturales (FARN), Argentina

Argentine provinces hold to themselves all the powers not expressly delegated to the Federal State by the National Constitution. Wild fauna management is an example of an undelegated power and, as such, it depends on Provincial States.

Under the Argentine Civil and Commercial Code, wild animals are regarded as ownerless property (*res nullius*), acquirable by appropriation through legal hunting or fishing. If wild animals are in areas controlled by the National Parks Service, they are owned by the Federal State. However, they reacquire their ownerless property status outside of those boundaries, provided that no malicious act was committed.

The Federal Law 22,421 on wild fauna conservation, passed in 1981, provides for the protection of wild fauna and its habitat, its use, trade and hunting, and issues regarding animal health. It states that "*all inhabitants of the Nation have a duty to protect wild fauna […]*". However, it is only applicable to those provinces that have ratified it by law. The exceptions are Sections 24 to 27 (Criminal Acts and Penalties Chapter), which are applied nationwide and are mandatory even in provinces that have failed to ratify it. This is due to the fact that, pursuant to the National Constitution, criminal laws shall only be enacted by the Federal State, and not by Provincial States (delegated power). Thus, hunting species whose capture or trade is forbidden is deemed to be a criminal act in Argentina, as well as hunting on land owned by third-parties with no authorization or with banned guns, gear or means.

Now, the new paradigm brought about by environmental law – which Argentina enshrined in its 1994 Constitutional Amendment and which was followed by the enactment of various federal environmental protection laws – means that wild fauna cannot be reduced to a mere thing that may have economic value, but also its ecological and intrinsic value needs to be acknowledged.

(continued)

Box 6.1 (continued)

Argentina's wild fauna falls under Sect. 41 of the National Constitution, which states, on the one hand, that all inhabitants have a duty to preserve the environment; and, on the other hand, that authorities shall provide for the "*rational use of natural resources, the preservation of the natural and cultural heritage and of the biological diversity*". In addition, the National Constitution acknowledges the right of indigenous peoples to manage natural resources available in lands traditionally occupied by them (including wild fauna and its use).

Even though ideally Argentina should update Law 22.421, and list wildlife as a national and state heritage (public domain) in order to facilitate conservation and responsible use policies, the fact is that wildlife is an integral part of the environment. Consequently, it now falls within the protection framework of the environment as a collective good, and an integral, exosystemic, conservation and sustainable use approach must be applied, with full respect for its intrinsic value.

indigenous and low-income rural communities by the State and the promotion of private property over common property (Lichtenstein 2013).

6.3 The Socio-productive Context in Patagonia

The current pattern of land occupation in Patagonia, as well as the established power relations, respond to a history of appropriation by the national State of the land that was originally occupied by indigenous people (Chap. 2). In this way, by dispossessing the original communities of their natural means of subsistence and transferring them to new owners, the foundations of a different social structure were laid. In this new scene, a different relationship between the new settlers and the environment was established in which Nature became a source of resources to be exploited in order to maximize short term income (Bandieri 2018).

At the end of the nineteenth century, the Argentinean government launched the "Desert Campaign" (1879–1885), a military campaign to Patagonia, with the aim of expanding the economic frontier and promoting Argentine's state formation and consolidation. The lands previously occupied by indigenous communities were appropriated by the State as "public lands" and transferred or sold to a few private landholders, thus creating a concentration of land for extensive sheep wool production (Bandieri 2005). Thousands of indigenous people were methodologically subdued, killed, evicted or relocated to reservations in inhospitable and isolated places, destroying most communities and their previous relationship with the natural environment (Chaps 2 and 9, Bandieri 2005).

After the “Conquest of the Desert”, immense extensions until then occupied by the indigenous communities became fiscal patrimony. In 1884 Law 1532 was enacted, which created the national territories of Chubut, Neuquén, Río Negro, Santa Cruz and Tierra del Fuego. The limits, surfaces, forms of government and administration were thus defined (Coronato 2010). According to Bandieri and Dabus (2019), access to public land in the Patagonian territories was basically achieved in four ways: the first contemplated the condition prior to colonization and settlement by application of Law 817 of 1876, (then eliminated by the Law 2875 of 1891 that transformed the colonists into permanent owners); the second through public auctions (Law 1265 of 1882); the third by the Home Law (Law 1501 of 1884); and the fourth by the possession of military award certificates that awarded lands to those who had taken part in the conquest (Law 1628 of 1885). The “Home Law” tried to create agro-pastoral colonies in the national territories, handing over land to indigenous groups surviving the Conquest of the Desert. However, the lots of just 625 hectares in the most arid regions were already too small for extensive livestock ranching under the Patagonian environmental conditions, and thus the productive insufficiency only accentuated the poverty of these defeated peoples that continues today (Coronato 2010). In addition, the subsequent growth of human populations and that of animal populations supporting them increased the grazing pressure on the scarce natural resources of the settlements, leading to an aggravation of the desertification and biodiversity loss processes (Golluscio 2010).

The state policy of land distribution was characterized by almost complete ignorance of the agro-ecological characteristics of the lands handed over, and the promulgation and manipulation of regulations for the benefit of influential individuals (Bandieri 2018). This resulted in a region with great contrasts in relation to the agrarian structure: a strong presence of small producers in the irrigated areas, and few producers with large surfaces in the dry areas dedicated to extensive livestock ranching resulting in 94% of the surface being in the hands of 30% of the production units (EAPs[2]) (Sili and Li 2013).

According to the 2010 National Census, in Patagonia 145,000 people self-recognize as descendants or belonging to an indigenous people. This figure represents 6.8% of the regional population, constituting the region with the largest indigenous population in the country.

In summary, land tenure and occupation have been factors of conflict in the history of the Patagonian provinces since the nineteenth century. From the point of view of agrarian structure, land distribution is far from being equitable with the highest proportion of large-scale extensive livestock operations in the country (IFAD 2011). It is in this landscape of private property, fences, and large sheep ranches that most of guanaco populations are present and management operations on the species take place.

[2] EAPS are the statistical unit of the National Agricultural Census, and refer to the organizational unit of agricultural production with at least 500 m2 within a single province, regardless of the number of parcels.

6.4 Stakeholder Analysis

The use of wild guanacos in Patagonia presents an intricate scenario of stakeholders that responds to the social-environmental complexity of the current production system. This multiple and diverse network involves government agencies with different levels of hierarchy, availability of financial resources, and different access to producers, and therefore the possibility of exercising different power over decision-making; producers with different socio-economic background and realities, including diverse situations of land ownership on which their productive activities are deployed; and also with different historical and cultural characteristics that motivate dissimilar interests. Finally, this stakeholder network is made more complex by the presence of fibre traders, as well as by designers and artisans in the local market (Fig. 6.1).

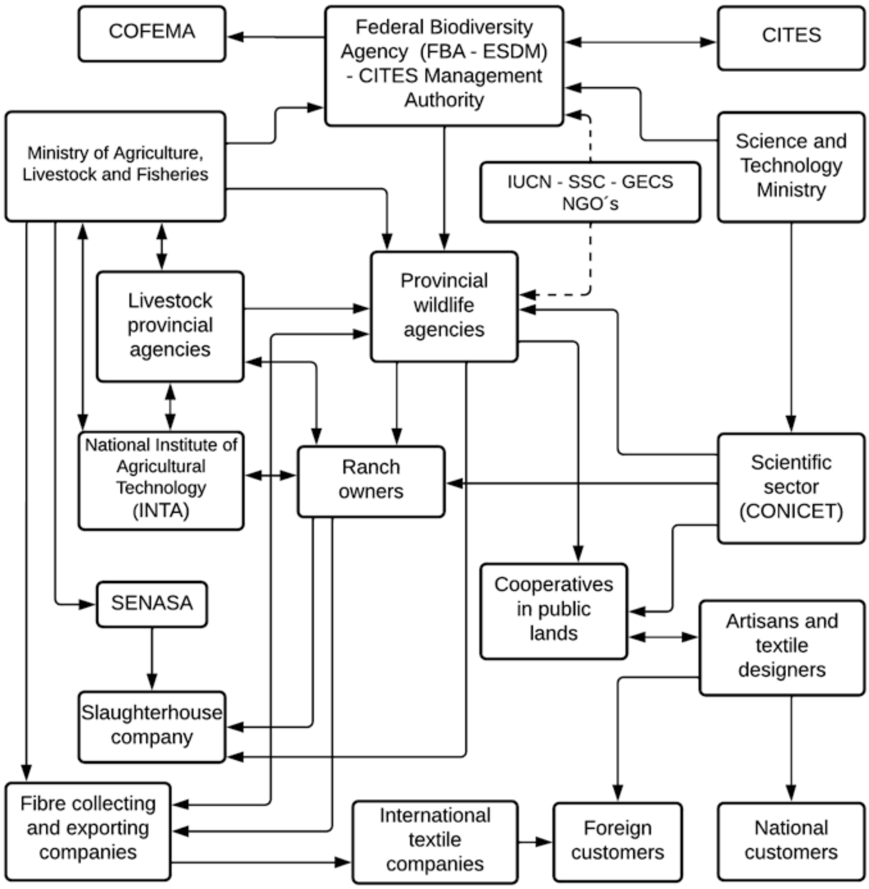

Fig. 6.1 Stakeholder mapping for guanaco management in Argentina. The dashed line between the wildlife agencies and IUCN/NGOs indicates that it depended on the political will of the enforcement authorities

At international level, an important stakeholder in shaping guanaco use in Argentina was the Convention on International Trade of Endangered Species (CITES). This is an international agreement between governments that aims to ensure that international trade in specimens of wild animals and plants does not threaten the survival of the species. CITES provides a framework to be respected by each state that agreed to be bound by the Convention (called Party), which has to adopt its own domestic legislation to ensure that CITES is implemented at the national level.

The national enforcement authority regulating wild guanaco management activities in Argentina is the *Dirección Nacional de Biodiversidad* (Federal Biodiversity Agency, FBA) which depends on the *Ministerio de Ambiente y Desarrollo Sostenible* (Environment and Sustainable Development Ministry, ESDM).[3] This Ministry is also the Management authority for CITES. The FBA assists in the technical aspects of the formulation and implementation of environmental policy for the knowledge, conservation and sustainable use of biodiversity, access to genetic resources and the fair and equitable distribution of the benefits derived from their use. The FBA is a member of the Federal Environmental Council (COFEMA), which is a forum for the coordination of environmental policies in which, in addition to the national government, the provinces participate. The FBA played a leading role in the development of the first National Guanaco Management Plan (NGMP 2006), together with the wildlife administrations of Chubut and Río Negro provinces. However, the policies followed by these agencies changed according to the succession of different government administrations and were influenced by other national agencies such as the Ministries of Agroindustry and Production (from 2020 they were called Ministry of Agriculture, Livestock and Fisheries, and Ministry of Productive Development, respectively), by the livestock agencies of some Patagonian provinces and lobby by the private livestock sector. This influence resulted in the modification of the NGMP carried out in 2019 which was also favoured by the actions of technical agricultural development agencies, such as National Institute of Agricultural Technology (INTA), which has direct access to producers and a productivist approach to the use of free-ranging guanacos.

The policies developed by the FBA are generally adopted by the provincial wildlife agencies. In some provinces, these agencies are included within the livestock administrations, for example, in the provinces of Chubut and Santa Cruz. Therefore, these provincial wildlife departments are in a weak position and have a strong influence exerted by the livestock sector. In provinces such as Mendoza, Neuquén, and Tierra del Fuego, these departments are located in the Environmental area; in these cases, the influence from the livestock sector is not so strong. The provincial wildlife agencies have the function of implementing policies in relation to the species and conducting law enforcement on guanaco management.

[3] The Environment and Sustainable Development Ministry as well as the Ministry of Science, Technology and Productive Innovation were downgraded to Secretaries during the Macri administration (2015–2019).

Another national government agency that has played an important role in the development of the management and monitoring system for the species is the Ministry of Science, Technology and Productive Innovation through its scientific bodies such as the National Council for Scientific and Technical Research (CONICET), which has influenced both national and provincial public policies. As mentioned in Chap. 7, several scientific studies have contributed to the development of protocols for good management practices. These protocols have served as a basis for the elaboration of provincial and national regulations such as management plans. The scientific sector has also supported the development of management activities for ranch owners and low-income cooperatives. This support not only took the form of technical activities, but also provided links with the textile and fashion sector. However, in the reformulation of the Guanaco National Management Plan in 2019 (see Sect. 6.4), the opinion of this sector was not considered by the public organizations that carried it forward.

The beneficiaries of the use of the species are the producers, who can be divided into two distinct groups: those who are large landowners, and those who are occupants of public lands. The main activity of the first group of producers is large-scale sheep production and, therefore, the income that can be generated by the production of guanacos is a complementary source of minor importance. With a few exceptions, these ranch owners ("*estancieros*") have followed the logic of "invest little and earn a lot" in relation to guanaco use, with little concern for animals' welfare. Ranch owners mainly sell fibre in its raw state to one of two stockpiling companies with a long history in Patagonia of exporting natural fibres, which then add some value by dehairing and exporting it. These companies also buy sheep wool from the same producers and thus have well-established contacts. The companies export guanaco and vicuña fibre, mainly to Italy, where it is processed into finished goods for a niche market.

In the case of meat production, these producers are associated with a meat processing factory. The animals are either slaughtered at the place of handling or transported in trucks to a slaughterhouse. The activity is overseen by the National Service on Health and Agri-food Quality (SENASA) and by the Provincial Wildlife Agencies. The income generated by meat production is restricted to the owner of the ranch and the slaughterhouse.

The main activity of the second group of producers, with precarious land tenure and a subsistence economy, is goat and sheep husbandry at small scales. In this group, the income from guanaco use could be significant as a complement to their annual income (e.g. Lichtenstein and Carmanchahi 2012, 2014; Dreidemie 2018, Chap. 7). These producers do not have the means to start a guanaco management activity on their own and, therefore, were assisted by the provincial and national governments as well as the scientific sector in training and provisioning of materials and equipment. The high quality of the guanaco products, such as dehaired fibre or spun guanaco yarn, encouraged local textile designers to develop collections aimed at a specific public interest on this type of weaving and its history, although still operating at a small scale. The creation of local Cooperatives for guanaco management had not only an economic impact, but also non-economic benefits such as community empowerment, capacity building, community integration and political visibility of remote and forgotten pastoralists (Lichtenstein and Carmanchahi 2012, 2014).

For all producers, the corresponding provincial fauna authority grants the ownership of the fibre by means of a Certificate of Origin and Legitimate Electronic Tenure (COLTE in Spanish), a document that accredits the legal tenure during all stages of elaboration and industrialization of products and sub-products. For transit between jurisdictions of any guanaco product or sub-product, the producer must obtain the Unique Electronic Transit Guide, which is also issued by the provincial state but is provided by the FBA. In case of export of these products, it is also required to obtain a CITES permit from the national authority (FBA). If a partial sale is made, the producer deducts the weight sold from the quantity originally certified through the COLTE.

6.5 Background 1978–2002. Role of CITES in the Commerce Restriction of Guanaco Products from Argentina

In 1978, after a request made by Peru, the guanaco was included in the Appendix II of the CITES which implied certain restrictions and regulations for its commerce. Even though the exploitation and commerce of the species was intense in Argentina in those years, the country ratified this Convention in 1981, becoming a full country member.

Based on the large numbers of guanaco pelts exported from Argentina (including calf's, called "*chulengos*"), the Fauna Committee at CITES requested to Argentina in 1992 an explanation about the biological basis employed to justify the exploitation of the species as well as the enforcement procedures involved in the control of exports of guanaco products. At that time Argentina was unable to answer those inquiries from CITES, which triggered in 1993 the CITES recommendation to all country members to suspend imports of guanaco products from Argentina until the country presented an appropriate management plan.

In those years, several activities started to develop in the Patagonian region because of a growing interest in the wildlife provincial authorities about the guanaco and potential management techniques. Gradually the scientific and technical sector began to participate in a series of meetings and workshops under the leadership of the Patagonian Wildlife Advisory Council (CARPFS, under its Spanish acronym) in which tasks and criteria regarding the guanaco were coordinated. Two meetings held in 1996 and 1997 were the first steps that initiated the discussion of technical foundations and criteria for a future management plan, including specific approaches to harmonize the legislation in the different provinces.

In 1998, the Federal Government dictated Resolution 220, which generated a halt in the regional activities regarding the guanaco that were taking place in the

Patagonian region. This resolution banned the export, commerce in the federal jurisdiction and the transit of guanaco products between provinces, until a guanaco management plan could be elaborated. The intended period for the elaboration of the mentioned plan was one year (the plan was approved in 2006). However, the resolution had three exceptions: (1) stocks of guanaco pelts recorded at the Provincial Wildlife Agencies and the FBA prior to February 1994; (2) products of guanaco obtained through experimental live-shearing of guanacos properly recorded and generated during the phases of elaboration of the management plan; and (3) guanaco products exported without commercial purposes, aimed at industrial tests of the fibre, up to a maximum of 500 kg for each company. The interruption of activities continued until 2000, when a technical forum met to define survey methods, marking systems and minimum contents of the management required at the captive units of guanacos. The recommended guidelines for population surveys were included in Annex I of Resolution 82/2003 dictated by the Federal Government.

6.6 First National Guanaco Management Plan (2006)

The process that ended with the first National Guanaco Management Plan (NGMP) for Argentina in 2006 (Baldi et al. 2006) was driven by several factors and stakeholders, relevant to that historical moment, that helps us understand the final product achieved. During the final years of the 1990s and first years of the twenty-first century, there was an increasing number of experiences that started to explore the feasibility and potential effects of live-shearing on the behaviour, demography and welfare of guanacos (Montes et al. 2006; Carmanchahi et al. 2011, 2014). The provinces where the majority of initiatives took place were Río Negro, Neuquén, and Mendoza, with a limited initiative in Santa Cruz. On the other hand, it was starting to become apparent the steady and gradual increase in guanaco populations inhabiting the southernmost provinces of Chubut, Santa Cruz, and Tierra del Fuego due to different reasons (see Chap. 1).

In 2002 a couple of technical meetings among Patagonian provinces and the Federal Biodiversity Agency took place, in which different management experiences were presented, including the identification of a new legal inclusive framework that was needed to replace some partial and limited legal norms (Resolutions 220/98 and 82/2003) aimed at regulating the first live-shearing projects that were being developed, as well as captive breeding facilities. Finally, in 2004, the provincial authorities of the Patagonian provinces led by Rio Negro and Chubut envisioned the urgent need to discuss and elaborate a Guanaco Management Plan for Argentina, with the objectives of providing an ampler and comprehensive framework for the sustainable use and economic benefit from the species, and also to cope with the growing concerns of ranchers due to the increase of guanaco numbers. We have to recall that Chubut province was the main source of guanaco pelts of adults and young guanacos during decades (Chap. 1; Ojeda and Mares 1982) and there was a tradition among sheep herders to count with a mechanism in place that reduced guanaco numbers and limited competition with livestock according to their vision (S. Rivera, pers. comm.; Baldi et al. 1997).

The elaboration of the management plan was advanced through two workshops and the further work was conducted by an editorial committee appointed by the group of participants. At both workshops, the main attendees were members of the technical and political areas of the Patagonian provinces (Chubut, Mendoza, Neuquén, Río Negro, Santa Cruz, and Tierra del Fuego), members of NGOs involved in guanaco research and conservation, researchers at CONICET, professionals from the Federal Biodiversity Agency, and the Ministry of Agricultural, Livestock and Fisheries, and members from the National Institute for Agrarian Technology (INTA).

The National Guanaco Management Plan was approved in 2006 by Resolution 477 of the State Secretary of Environment and Sustainable Development declaring an overall goal of ensuring guanaco conservation, in particular, the viability of wild, ecologically functional guanaco populations and the persistence of the species throughout its geographic range (Baldi et al. 2006). The first provinces to adhere to the Plan were Chubut and Santa Cruz, which hold the largest guanaco populations in the country. Gradually, the remaining Patagonian provinces adhered to the plan, with the exception of the province of Rio Negro.

The plan included guidelines for guanaco management through live-shearing of free-ranging animals and productive units in captivity. Requirements for inspecting shearing practices and high animal welfare standards during shearing were also included. It established surveys as mandatory before and after the shearing operation, with details on technical aspects of the survey recommended methodology.

The strengths of the elaboration of the first National Guanaco Management Plan were: (1) the initial steps were led by the provinces with the largest guanaco populations; (2) it was the first management plan for a wildlife species that considered some type of use (until 2006 the only other national management plan in Argentina was elaborated for the Huemul – *Hippocamelus bisulcus* –, strictly focused on protection due to its conservation status); (3) the technical and scientific sector had a strong voice, which can be appreciated in the extensive scientific data used as a background for the plan; (4) the last phases of the plan were conducted by an editorial committee that was able to consider all the observations and comments from the rest of the participants, with a real horizontal process, at least for the participants involved; (5) an updating mechanism for the plan, at least every 5 years, was specifically mentioned; (6) due to the federal nature of the country, all the provinces encompassed in the guanaco range were invited to adhere to the plan through their specific mechanisms in each case.

However, the plan also had several drawbacks, as follows: (1) neither local ranchers nor local communities co-existing with guanacos in Patagonia were invited to participate in the process, following a top-down model (Lichtenstein 2013); (2) despite being a Plan intended for the whole country, the participation of the provinces outside the Patagonian region, that need strict protection policies for their guanaco populations, was almost insignificant; (3) no participation was granted to governmental areas that need to be involved in the development of markets for guanaco products, one of the weaknesses for profitability of guanaco management; this issue became apparent in 2010 when most of live-shearing operations stopped because of marketing difficulties (Lichtenstein 2013); (4) regardless of the marked increase in guanaco populations in the Southern provinces (Chubut and Santa Cruz), the plan did not address in detail the guidelines, requirements, enforcement needs, sanitary aspects, marketing issues and technical constraints of a management scheme focused on guanaco harvest able to generate meat products for the local and international markets.

We can conclude this section by mentioning that although the first National Guanaco Management Plan represented a turning point from a historical point of view of wildlife management in Argentina, the apparent limitations that it showed reduced its potential application and efficiency in order to manage and conserve the guanaco populations.

6.7 Provincial Management Plans: Chubut and Santa Cruz

Before 2006, sheep ranching in Patagonia was already going through an important crisis, magnified by reduced pasture productivity caused by a lasting history of overgrazing (Del Valle et al. 1998, Aagesen 2000, Mazzonia and Vázquez 2009). Desertification was caused by, both, climate change and historic inappropriate grazing management, which resulted in a diminished carrying capacity (Golluscio et al. 1998; Andrade 2013). Declining profitability was also related to the decrease in wool price, and a rise in grey fox (*Lycalopex griseus*) and culpeo fox (*Lycalopex culpaeus*) populations which had a high impact on sheep mortality (Funes et al. 2006). As soon as the 2006 guanaco management plan was approved, a number of ranchers were already against it (Von Thüngen 2009). They endorsed the guanaco full responsibility for their problems, as they traditionally considered the species a competitor for consuming all the grasses and water they reserved for sheep (Caro et al. 2017). Interestingly, sheep ranchers did not take into account the impact of their own production practices on natural pasture and desertification (Andrade 2013).

With this plan enacted, Patagonian producers got even more worried about the recovery of some populations of guanaco, and the potential competition with their sheep for winter grasses, and the worrisome presence of herds nearby the long stretching roads of the Province. Having hunted down the puma (*Puma concolor*), the natural predator of the guanaco, they saw in the 2006 guanaco management plan a deterrent for the human control of guanacos.

Making use of their encumbered social position, producers against the NGMP were readily able to convince the provincial authorities to develop a provincial plan that would include guanaco culling products. This was relatively easy as in some cases the higher authorities of provincial wildlife management offices were part of those producers (see Sect. 6.4).

The Province of Santa Cruz approved a law to develop a Sustainable Management Plan for Guanaco (Law 3039/2008) that considered the use of fibre and meat of the species. The INTA supported this initiative as they considered these items as diversification products for the progress of the rural sector, and a way of portraying the culling of guanacos to the public as a more acceptable "integral use" than just a mean of controlling the alleged overpopulation of the species (Von Thüngen 2009).

With a contrasting approach, the province of Chubut started a consensus building series of workshops between the interested sectors to arrive at a management plan in 2012. The plan was embedded in the adaptive management approach, which contemplated periodic instances for evaluation and adjustment (Holling 1978). Gourmet meat tasting sessions took place in the Province and the properties of guanaco leather were assessed. The plan also included the development of a, much criticized by the scientific sector, ad-hoc harvest model to indicate the number of guanaco individuals that could be culled from a single sheep breeding ranch.

Along that same year, the House of Representatives of the province of Santa Cruz requested the Provincial Executive Branch and the Provincial Agrarian Council (CAP) to declare guanaco as a harmful species for being a concern for vehicular accidents, and producing economic damage. By the end of 2012, the province of Tierra del Fuego, passed a law to create a Sustainable Management Plan for Guanaco (Law 919/2012), a literal copy of the Plan passed by Santa Cruz in 2008. Both provincial laws demanded information to develop a captive animal stock and the management of free-ranging individuals, as well as methodologies to avoid collisions with vehicles. The Tierra del Fuego law was never implemented.

Later in 2014, the province of Santa Cruz elaborated a guanaco management plan (Provincia de Santa Cruz 2014). It included an estimation of guanaco abundances (Box 6.2) and a new version of the harvesting model used for Chubut. Both were criticized by the scientific sector for the lack of scientific rigour. In this plan the guanaco is blamed for all the problems the producers traditionally had, such as the desertification of Patagonia: "one of the main reasons for the reduction of sheep numbers was the uncontrolled increase of guanaco" and the need to "tackle the guanaco problem" (La Nación 2017). Although restrictions were incorporated to the culling model first presented for Chubut, the underlying concept still was that the guanaco was a pest to be controlled. In a similar fashion as the plan of Chubut, this plan also contemplated the use of fibre, leather and meat.

In 2017, with less than a month in between, two exceptions to the 2006 national plan were passed: the first one allowed the inter-jurisdictional transit of meat, obtained from 200 guanacos from the province of Santa Cruz (Resolution 711/2017 MAyDS), while the second exception considered transit of all kind of products (i.e. fibre, leather and meat) obtained from 6000 individuals from the same province (Resolution 766/2017 MAyDS).

6.8 National Guanaco Management Plan (NGMP) 2019

As mentioned above, the update of the NGMP started to be discussed by the productive sector shortly after its approval, as it can be perceived by the regulations promoted by Santa Cruz (2012) and Chubut (2012). During 2011, a multisectorial workshop identified the need to adjust the NGMP to the needs and reality of each province, still with the goal of maintaining healthy guanaco populations.

At regional workshops held in 2014 and 2015, Santa Cruz and Chubut wildlife authorities requested the Federal Biodiversity Agency, new management options for the guanaco from a national level in order to accompany their plans at the provincial level (Sect. 6.7). This was accompanied by a lobby campaign against guanacos supported by the media, including newspapers and radio programmes that managed to create the narrative of guanaco overpopulation and the alleged negative consequences that it generated.

The lobby was well received by the recently elected neoliberal government who was prone to attend to the needs of private sectors. The results of the November 2015 run-off presidential elections in Argentina marked the beginning of a historic turning point in moving from a centre-left to a centre-right government. With the advent of the new government the budgets for science, technology, health, environment and education (as well as social welfare) were reduced and over a thousand state employees were dismissed (Amescua 2020).

By mid-2016, the FBA started updating the NGMP, in order to authorize new extractive uses, even with the potential collision with uses promoted by other provinces (Mendoza and Río Negro) under the 2006 NGMP for more than a decade. Therefore, still under a participatory process, different sectors agreed on the need for: a revision of the NGMP 2006; new uses for fibre and meat by pilot experiences; protocol update (good management practices, animal welfare, added value, among others), inclusion of a commercial development component; resuming the abundance and distribution assessment at a regional or national level; an Operational Plan for the NGMP; development of new markets for guanaco products and by-products; strengthening authorities and capacity building for law enforcement and monitoring; resolving regulatory voids and contradictions between jurisdictions; consensus in the methodological and technical criteria for inclusion in the NGMP.

By mid-2017 an "interinstitutional working group" was created by the Federal Government, with political representatives from the Secretariats of Planning and Policies in Science, Technology and Productive Innovation; of Agriculture, Livestock and Fisheries; of Entrepreneurs and SMEs; the National Institute of Industrial Technology (INTI) and CONICET on top of the Secretary of Environment, and the National Service for Agrifood Health and Quality (SENASA) with the stated aim to develop commodity chains and technologies for guanaco sustainable use. Although the project design was led by the Science and Technology Ministry, it did not have effective participation from its main research body, CONICET, nor researchers. The project was narrowly open to contributions and suggestions, through inorganic and spasmodic processes.

A pilot project to harvest 6000 guanacos from Santa Cruz in order to obtain meat and fibre was developed between the "interinstitutional working group" and the private sector (slaughter house, fibre processor). This project was later presented as the main input for the update of the NGMP, which was expected to be completed by the end of 2017. This intended schedule revealed another essential feature of this process: the ignorance of the authorities about the logistical, biological and instrumental complexities to advance from a project prepared on desk to a medium-scale intervention in a wild species population over a large landscape like Patagonia.

To overcome the 2006 NGMP, the Secretary of the Environment and Sustainable Development exempted the export of guanaco by-products from Santa Cruz, framing the exception in the "Guanacos Sustainable Use Project" without the development of an operative plan. The project implementation window moved to 2018, planning the harvesting for March, when females are nursing the calf born a few months ago and are pregnant again, which implied sacrificing three animals at the same time, potentially affecting the productivity of the population.

The strategy chosen by the project promoters was to abandon the intersectoral workshops that had accompanied this process for nearly eight years. They moved to a strategy of separately convening stakeholders to "present" the project and receive comments that were later to be "addressed". The project, as such, continued to be known only as "drafts", on which opinions were sought. The provinces, as responsible for wildlife management, were not formally aware of the project and did not intervene in its drafting, with the exception of the province of Santa Cruz, in spite of the implications of the contradictory uses that would affect management operations of live-shearing authorized by other provinces.

In March 2018, the Chair of CONICET asked a group of researchers specialized in guanaco conservation and sustainable use to provide their views on the project. The scientific sector warned that conducting a pilot test in isolation and uncoupled from a structure of "questions" to be answered through management and without clear indicators to be measured, carried the risk of providing incomplete answers of limited generalization, thus threatening future alternatives for guanaco management. For this reason, the researchers recommended developing a medium and long-term program of experimental management for the guanaco, which would provide the necessary inputs to assess the viability of a guanaco sustainable and consumptive management, with all the needed advances of the technological, ecological, social and economic issues. This document was dismissed.

The Santa Cruz pilot test was finally carried out between June and October 2018. In September 2018, a draft of the "updated" National Guanaco Management Plan began to circulate, which was sent to different NGOs. An inorganic consultation and participation process continued, prioritizing contact with other stakeholders against the scientific and technical sector. The new Plan presented a short summary of the results of the Santa Cruz Pilot Project. This was so short and unclear that it was difficult to evaluate its achievements, the biological consequences of the interventions, and the applicability of the results to move to a scale of extensive use.

The results of the Santa Cruz Pilot Project were formally presented by the Secretary of the Environment and Sustainable Development at the end of 2018 to different stakeholders, who expressed concerns about various issues, such as:

- The clear leadership of livestock sectors without knowledge about wildlife ecology and management, focusing on assimilating the guanaco as livestock.
- The lack of compliance with animal welfare standards.
- Aptness of the auditors and of those who carried out the project, who lacked personnel with expertise in wildlife management and animal welfare.
- The lack of traceability and transparency throughout the value chain.
- The mixture of fibres from dead and live animals, threatening experiences of live-shearing in the wild under high standards of animal welfare (neither the transit guides nor the CITES permits discriminated against the source of the fibres).
- The lack of external observers during the experiences.

The final report of the Santa Cruz Pilot project was made public in November 2019. It provided incomplete and contradictory information, reducing its value as an input for a radical modification of the NGMP as it was warned before. In other areas, such as animal welfare and traceability of products, the report was poorly informative.

Finally, in April 2019, the updated NGMP was opened for public consultation, through the website of the Secretary of the Environment and Sustainable Development.[4] Almost at the same time, the provinces with guanacos in their territories learned about the final national plan, producing great discontent in the jurisdictions that, with the exception of Santa Cruz, had not participated in the generation of this new plan.

Despite the large number of critical comments made by different sectors of the community, the new National Guanaco Management Plan was approved by Resolution 243 of the then Ministry demoted to Governmental Secretary of Environment and Sustainable Development in July 2019,[5] with the same text that was put for consideration in the open consultation. None of the comments provided in the open consultation were taken into account, rendering the consultation process useless.

- The new Plan presented the results of the Santa Cruz pilot experience as one of the central foundations for updating, when the results of that experience had not been validated by any instance of exchange of opinions either with other jurisdictions or with the scientific sector.
- The Plan outlines uses for the guanaco and establishes a series of obligations or responsibilities for the provincial states, being unaware of the need for strengthening of the provincial authorities. This weakness favours the illegal use of the

[4] https://www.argentina.gob.ar/noticias/consulta-publica-para-actualizar-el-plan-de-manejo-del-guanaco

[5] https://www.boletinoficial.gob.ar/detalleAviso/primera/210794/20190704

species, the development of black markets, in addition to not having information about the use to monitor and plan future uses.

- The Plan did not include references and provisions on how to reconcile contradictory uses of guanaco between jurisdictions.
- The Plan did not make it clear that the export of live animals or genetic material will be forbidden, nor does it refer to the destination of fibre from dead animals.
- The Plan proposed "to identify the information gaps necessary for the management of the species, considering both its use and its conservation including the evaluation of the effectiveness of protected areas with the presence of guanacos and the need to create new protected areas…". These statements reflect a vision of a landscape where guanacos are "safe" from extractive uses only inside protected areas. It is currently recognized that its conservation within protected areas must be complemented with conservation outside protected areas, by seeking the coexistence of production with biodiversity in the same landscapes, through various strategies such as the search for differential markets for products from "friendly" livestock practices with the environment. Achieving heterogeneous production landscapes, with large and structurally complex patches, connected in a matrix that tries to preserve structural characteristics similar to those of native vegetation, promotes sustaining a diversity of processes such as the maintenance of populations of key or threatened species, the control of invasive species, and greater resilience to extraordinary events.
- In the line above mentioned, the NGMP did not define actions in areas where populations have serious conservation problems and need strategies focused on protection.

The main consequences of the Plan currently in force have been the potential increase of poaching, the promotion of a black market for guanaco fibre and meat (meat offered even in social networks), the existence of a double fibre standard, all in a context of persistent institutional weakness of the provincial authorities, some of which are now trying to imitate what was done by the Santa Cruz pilot project.

At the end of 2019, the change of the national government brought a political orientation with a stronger influence of the state in the management of natural resources. A window of opportunity opened to raise the need to modify the NGMP. Thus, at the beginning of 2021 the environmental authority announced the review of the plan, through a much more participatory process than the previous one. However, by mid-2021 there has been no progress.

During the process that led to the new NGMP, several advisory boards and sectors of the society (e.g. the National Advisory Commission for the Conservation and Sustainable Use of Biological Diversity (CONADIBIO), the Advisory Commission for Biodiversity and Sustainability (CAByS), IUCN's South American Camelid Specialist Group (IUCN SSC GECS), the Argentine Committee of the IUCN, scientists with expertise in the biology, ecology and management of guanaco, NGOs (e.g. Greenpeace, WCS), and some provincial jurisdictions, among others), tried fruitlessly that the review process involved a more participatory mechanism including different perspectives and visions about a widely distributed public resource. The strategy chosen by the national government at that time privileged the interests of a sector of society, pretending to apply a participatory process to disguise it, as shown by what is narrated here.

6.9 Attempts to Install a Productive Livestock Agenda on Wild Camelids

Along the recent history, several law projects have been passed by, both, the Deputies and Senators Chambers of the National Congress to promote the production of South American camelids without distinguishing between domestic (alpaca – *Vicugna pacos* – and lama – *Lama glama*) and wild species (guanaco and vicuña –*Vicugna vicugna*). In these projects, the designated enforcing authority was the Ministry of Agriculture, Livestock and Fisheries (MAGyP), thus, disregarding previous national and international laws that indicate that, at the national level, the Ministry of Environment and Sustainable Development (MAyDS) is the organism in charge of wildlife conservation and management. These projects were presented to the Commissions of Agriculture and Livestock, Budget and Finance, or Economies and Regional Development, but ignored the necessary intervention of the Commission of Natural Resources and Conservation of the Human Environment. Only the reaction of the environmental authorities, the scientific sector and NGOs put these projects on hold.

Following previous projects that included the term "camelid" with no reference to them being domestic or wild, and only three months after the sanction of the 2006 Guanaco National Management Plan (NGMP), the proposed bill for the Regime for the development of South American camelid livestock was provisionally approved by the Chamber of Deputies. This was an explicit attempt to change the enforcing authority for the management of guanaco (and vicuñas) from the Ministry of Environment and Sustainable Development to the Agriculture Ministry. The goal was to allow a more permissive management of the species, including all marketable production of live animals, meat, fibre, leather, milk, fat, semen, embryos or other industrial or artisanal products derived, as with any domestic livestock production, despite the extensive and particular needs of wildlife management, and genetic resource interests the country might hold.

Later, the Chamber of Deputies provisionally adopted the law Regime for the Promotion and Development of South American Camelids in 2008. As a consequence, after the claims of environmental authorities, scientists and NGOs, in 2009, the Federal Council of the Environment (COFEMA, by its Spanish acronym) passed a resolution expressing their rejection to any project of law for the promotion and development of South American camelids that would not except guanacos and vicuñas.

In 2013, a project of the Chamber of Deputies, introducing modifications to the sheep farming law ("Ley Ovina") included concepts regarding the recovery of sheep livestock, but also the incorporation of the regulation of guanaco together with the lama. The project considered the need of endorsement from the environmental authorities for the guanacos, but it still tried to include the guanaco within a domestic livestock management pattern.

Recently, in 2021, a project under discussion at the Chamber of Senators insists on transferring the guanaco and vicuña to the responsibility of the Agriculture Ministry for its management. These permanent attempts to include wild South American Camelids under the livestock sector have deep implications not only in terms of management and conservation, but also with regard to the access and appropriation of benefits derived from the use of wild species. What is at stake is natural resource governance. These laws subtract wildlife from the legitimate scope of provincial and national agencies and allow landowners to freely manage guanacos in their properties as if they were livestock.

6.10 Main Drivers That Led to Policies

For the purpose of this chapter, drivers are recognized as all the factors that, directly or indirectly, influence the development of policies with regard to guanaco use and conservation. Drivers may have negative or positive effects on public policies, and the same driver may influence different policies along the years, leading to synergistic, or antagonistic effects with other drivers. Drivers are usually disaggregated into analytic categories such as environmental, socio-political, economic, cultural, and scientific and technological (e.g. Millennium Ecosystem Assessment 2003). Environmental drivers are abiotic forces that have generally been regarded as beyond human control, such as disturbance caused by earthquakes, volcano eruptions or extreme climate events (floods, droughts); given the concept of the Anthropocene calls attention to the increasing degree to which human actions may be directly altering these systems, we prefer to refer to socio-environmental drivers. Indirect drivers operate more diffusely by altering one or more direct drivers and they include institutions and governance systems, land tenure, property rights as well as those emerging from indigenous and local knowledge systems, socially shared rules, internal migration, power relationships, legislative arrangements, international regimes such as agreements for the protection of endangered species, and economic policies (Bustamante et al. 2018).

Figure 6.2 shows the main public policies in relation to guanaco management developed after the CITES recommendation for the suspension of guanaco imports from Argentina (Sect. 6.1). These are the 2006 National Guanaco Management Plan; the Provincial Plans of Chubut and Santa Cruz, and the Guanaco National Management Plan 2019. The development and implementation of these policies was a result of socio-environmental, economic and socio-political drivers. The figure illustrates the multi-causal nature of public policies.

As mentioned in Sect. 6.2 and Chap. 2, in the nineteenth century a compulsory expulsion/slaughter of indigenous people took place in Patagonia with the “Desert campaign”. Indigenous communities and their knowledge were “replaced” by new settlers that had a different rationale for exploiting the environment, and local people were alienated from their local environment and cultural heritage. Traditional European farming activities imported into Patagonia did not consider the use of native species as complementary to introduced livestock production. Instead, guanacos were viewed as an obstacle to sheep ranching and thus killed, either illegally or in accordance with government authorization (Baldi et al. 1997). Thus, a species that had been considered a vital resource for traditional local communities quickly became a nuisance animal for the colonizers. The policies of appropriation and re-distribution of land added to the unwise application of a productive model designed for wetter ecosystems (Coronato 2015) that did not include the use of native species (nor knowledge) were indirect anthropogenic drivers that contributed along the years to de-coupling the social-ecological system (Chap. 9), desertification and thus to increase the conflict between producers and guanacos.

The export of large quantities of guanaco pelts lacking a sound biological basis led CITES to recommend the suspension of guanaco imports from Argentina. The implementation of the NGMP 2006 was promoted by political drivers such as the request of CITES, agendas of the national government and provincial governments, but also by socio-environmental drivers. The climate crisis added to poor livestock practices and overstocking during decades had led to the degradation of grasslands, as mentioned in Sect. 6.3, which, combined with the crisis of the sheep wool market and the eruption of the Hudson volcano resulted in a progressive abandonment of fields, particularly in Santa Cruz and Chubut provinces (Andrade 2003, Fig. 6.2). At the time of the elaboration of the NGMP, sheep wool prices were very low and guanacos were perceived as an opportunity to generate an alternative source of income.

As soon as the 2006 NGMP was approved, a number of ranchers were already against it, endorsing the guanaco full responsibility for their problems. In the case of the provincial management plans for the provinces of Chubut and Santa Cruz, this was compounded by the growing conflict between the livestock sector and the guanaco populations. These also resulted from an increase in predator populations (Novaro and Walker 2005, Chap. 5) and recovery of guanaco populations due to the abandonment of ranches. The recovery of the guanaco populations in a scenario of increasing desertification intensified the conflict with the livestock sector and increased the negative perception of guanacos. These conflicts generated pressure towards the narrative of “integral exploitation” of guanacos (6.3) which was coupled with an environmental discourse of an alleged sustainable use (for marketing reasons).

In the case of the update of the NGMP in 2019, the provincial management plans of Chubut and Santa Cruz (formulated between 2012 and 2014) were an important foundation because they allowed the use of fibre and meat from dead guanacos. The

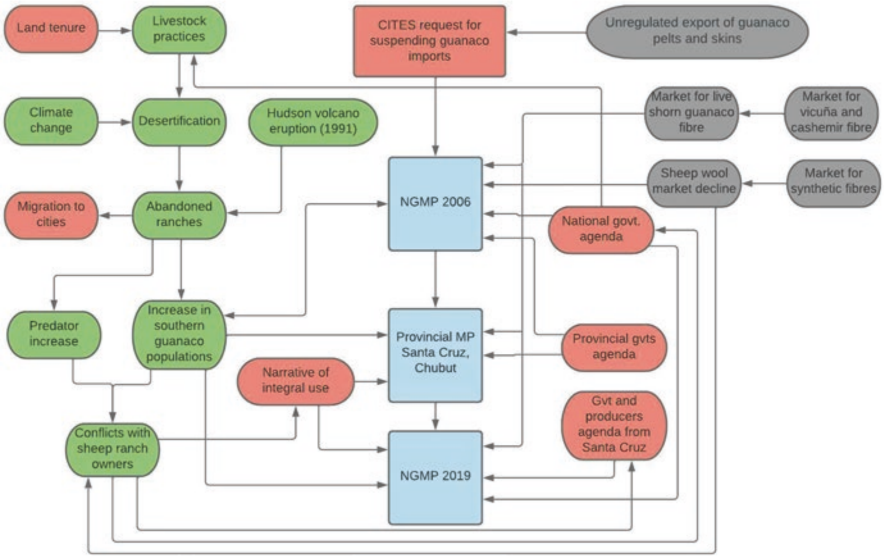

Fig. 6.2 Main socio-environmental (in green colour), economic (in grey colour) and socio-political (in red colour) drivers that shaped public policies after the CITES recommendation for the suspension of guanaco imports from Argentina. These are the 2006 NGMP; the Provincial Plans of Chubut and Santa Cruz, and the NGMP 2019 (all in light blue in the figure)

plan also resulted from the lobby of Rural Societies from Santa Cruz both on provincial and national authorities. Lobby also involved the media. The new government with a neoliberal orientation (2015–2019) strongly supported the update of the National Guanaco Management Plan and the creation of business opportunities for few enterprises (6.4). All along the years, local and national governments were more attentive to the voice of ranch owners than to the indigenous people, rural communities or researchers.

6.11 Final Remarks

Guanaco conservation and sustainable use in Patagonia illustrates the importance of approaching interlinked human and natural systems in a holistic way. The foreign productive model imposed in Patagonia resulted in severe desertification and conservation threats to wildlife and its habitat. A native species became a pest to the new settlers and this image persists today and is even promoted by livestock productive agencies, and accepted by some environmental authorities due to an unbalanced political strength and lobby capacity between sectors: Argentina has always based a large part of its economy on livestock and agricultural commodities.

Argentinean public policies with regard to guanaco management reflect the historical denial of indigenous and low-income rural communities by the State, and the promotion of private property over common property (Lichtenstein 2013). It also reflects the limited importance of nature conservation in the public agenda. The difference in power between different stakeholder groups enabled ranch owners to lobby and be heard while experts and local voices were muted.

The shift in policies with regard to guanaco management during the last thirty years in Argentina mirrors the multiple drivers involved in conservation and sustainable use initiatives. Direct and indirect economic, socio-political and environmental drivers were key in shaping policy. The story of guanaco management shows the need for strategic participatory conservation planning. Decision makers need to continuously monitor and integrate appropriate ecological, social and economic information into management as well as multiple voices that offer a variety of perspectives. It also shows the importance of devising long term policies in order to mitigate threats, exploit opportunities and maximize the likelihood of achieving the preferred outcome. The guanaco story also shows the enormous cost of making mistakes along these complex processes.

In 2021 the IUCN World Conservation Congress at its session in Marseille voted a resolution where it asks the Argentine government to: a) suspend the implementation of the recently approved NGMP in order to introduce changes aimed at guaranteeing the viability of the management of guanaco populations across its entire national distribution range, and the effective control of overexploitation and poaching; b) draw up, by consensus with all the sectors involved and the provinces in the guanaco's distribution range in Argentina, a revised National Plan for the management of the guanaco that takes into account the scientific background to the management of the species and its conservation status across its entire distribution range in that country; and c) ensure that the revised National Plan includes an effective traceability system for the trade that allows the fibre obtained from the live-shearing of guanacos to be identified and differentiated from the fibre obtained from the shearing of dead animals, the marketing of which is not recommended. Hopefully this time the new version of the National Guanaco Management Plan will have everybody on board.

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Chapter 7
Guanaco Sustainable Management as a Conservation and Rural Development Strategy

Pablo Carmanchahi, Gabriela Lichtenstein, Pablo Francisco Gregorio, Antonella Panebianco, Antonela Marozzi, Leonardo Leggieri, Fiama Peña, and Ramiro Ovejero

7.1 Introduction

Natural resources are essential for the livelihoods of thousands of communities, especially in developing countries (Turner 2004). However, these resources are being threatened on a large scale and are being used at a rate that exceeds their

The original version of this chapter was revised. The correction to this chapter is available at https://doi.org/10.1007/978-3-031-06656-6_10

P. Carmanchahi (✉)
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina
e-mail: pablocarman@comahue-conicet.gob.ar

G. Lichtenstein
Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires (UBA), Buenos Aires, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina

P. F. Gregorio · A. Panebianco · A. Marozzi · L. Leggieri
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina
e-mail: pablogregorio@comahue-conicet.gob.ar; apanebianco@comahue-conicet.gob.ar; antomarozzi@comahue-conicet.gob.ar

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_7

regenerative capacity by 30% (Dixon and Fallon 1991). Climate change, deforestation, land use for monocultures, open-pit mining, overgrazing, propagation of invasive species, species extinction, and alterations of hydrological cycles at local or regional levels, among others, threaten not only biodiversity but also the local values and livelihoods of millions of people living in extreme poverty who depend on the use of resources in their daily lives (Lichtenstein and Carmanchahi 2012). The benefits derived from the biological diversity at the ecosystem level provide multiple goods and services of economic and social importance (Andrade et al. 2011). The sustainable use of natural resources has the potential to ensure the persistence of these resources and contribute to improve the quality of life of local communities. Abundant empirical evidence indicates that for this to happen, it is crucial to guarantee legal access to resources, land ownership, generate incentives at the local level for sustainable management, empower local actors, and learn from traditional uses (e.g. Lichtenstein 2010).

Among the many challenges posed by sustainable use, the fair distribution of the benefits derived from resources remains elusive (Lichtenstein 2010; Lichtenstein and Carmanchahi 2014). Overcoming these challenges requires building the capacities of local communities involved in biodiversity management, establishing an adequate valuation of ecosystem resources, eliminating variables that detract from the value of these goods, and replacing them with local incentives aimed at achieving good management practices (Andrade et al. 2011). It is necessary to recognize the diversity of social and cultural factors influencing the use of natural resources and develop public policies for ecosystem management focused on biodiversity conservation and sustainable development.

Conflicts between wild species and human needs are some of the main threats to biological diversity in many parts of the world (Hill et al. 2002). This is most evident in grazing ecosystems, i.e. grasslands, savannahs, and prairies, where management imposes the greatest challenges. Large wild herbivores are mostly distributed outside protected areas, competing with livestock, and therefore are exposed to

F. Peña
Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina

Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA- CCT CONICET), Mendoza, Argentina
e-mail: fpena@mendoza-conicet.gob.ar

R. Ovejero
IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina

Instituto de Ecología Regional (IER), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Tucumán (UNT), San Miguel de Tucumán, Argentina
e-mail: rovejero@tucuman-conicet.gob.ar

poaching. In addition, state support aimed at benefiting unsustainable practices at the expense of biological diversity, through economic subsidies or taxation policies, is frequent (Norton-Griffiths 1995). In arid Patagonia, more than 95% of the land is privately owned, and most of it has been converted to sheep production since the late nineteenth century. The introduction of millions of sheep and the spread of traditional European practices led to severe habitat desertification (Bisigato and Bertiller 1997; del Valle 1998) and the decline of wild species such as the guanaco (Raedeke 1979; Puig 1995, see Chaps. 1 and 5). From a productive point of view, wild South American Camelids – the guanaco and the vicuña (*Vicugna vicugna*) – were recognized by the Food and Agriculture Organization (FAO) as key species for rural development in Latin America, based on their economic importance, the demand for their products, and the possibility of generating employment (FAO 1992).

The use of wild South American camelids could play a fundamental role in halting the desertification process of the arid ecosystems they inhabit, while at the same time providing an economic alternative for local producers. However, local producers and the predominant production system (i.e. livestock production) have a conflictive relationship with guanacos (Nugent et al. 2006), especially in areas with abundant guanaco populations. Conflicts related to interspecific competition manifested through dietary overlap, diet shifts, and spatial segregation (see Chap. 3) generate strong demand for management alternatives (Baldi et al. 2010). The search for solutions to the conflict generated between conservation and production paradigms, added to the high commercial value of the fibre in the foreign market, motivated the development of management modalities for guanacos in captivity and in the wild (Carmanchahi et al. 2011; Lichtenstein 2013). Consequently, methodologies for capturing, shearing, and releasing wild guanacos began to be developed in different Patagonian provinces (Montes et al. 2006; Carmanchahi et al. 2011). In this context, the generation of relevant biological information on the effects of management on physiological, behavioural, and population parameters was essential, since the manipulation of a wild species for its productive use can have negative implications at the individual, social, or population level, in the short, medium or long term. The evaluation of these impacts, taking into account multiple aspects and scales, is necessary to ensure the sustainability of a productive activity involving wildlife species such as the guanaco. In order for this productive activity to meet the criteria of sustainability, i.e. to be ecologically viable, economically profitable, and socially just (Holling 1993), it is also necessary to understand the socio-cultural and economic scenario in which the management of wild guanaco populations is introduced so that it becomes an economic alternative for the inhabitants with real possibilities of persisting in the long term.

In this chapter, we: (1) summarize the results of the research that established the scientific basis for the development of provincial and national regulations governing guanaco management; (2) analyse and compare economic contexts in different situations of management, whether through the use of wild guanacos by private enterprises and rural cooperatives or in captivity; (3) discuss the challenges that this activity still presents in the commercialization of its products; and (4) discuss whether the actions carried out since the elaboration of the Guanaco National Management Plan can be considered to have met the criteria for adaptive management.

7.2 Guanaco National Management Plan Background

As mentioned in Chaps. 1 and 5, the guanaco was an extremely important resource for the subsistence of the original inhabitants of Patagonia, being the main source of food and skins for awnings, coats, ribbons, and belts (Musters 1871; Moreno 1879; Mengoni 1996; Miotti 2012). European conquest brought with it the establishment of large ranches oriented towards extensive sheep production, with the consequent construction of fences and the elimination of wild herbivores and carnivores to limit competition and predation of livestock. However, the guanaco continued to be an alternative resource for rural dwellers through the capture of *chulengos* (calves) and the hunting of adults (Franklin and Fritz 1991; de Lamo et al. 1998; Funes and Novaro 1999). The skins of *chulengos* were used to make *quillangos* (blankets or coats made of hides sewn together), the meat of the adults was used to feed the herding dogs and the hides were used to make handmade cords and ribbons.

In 1978, the guanaco was included in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), which grants an export permit or a re-export certificate of products obtained from live shorn animals. Due to the high volume of guanaco hides and especially *chulengos* exported from Argentina, in 1992, the CITES Animals Committee requested Argentina to elaborate "the biological basis used for the exploitation of guanacos and to establish export control procedures". The CITES Management Authority in Argentina was unable to provide this information and, consequently, the CITES Steering Committee recommended during its 29th meeting in 1993 that imports of guanaco products from Argentina be suspended until a Management Plan for the species was submitted.

As a consequence of the ban, a series of actions were triggered involving different sectors, those interested in conserving the species and those who intended to benefit from the use of the natural resource. Finally, in 2006, the first Guanaco National Management Plan (GNMP) was approved by Argentine national government. This plan established management guidelines that regulated the export, interprovincial transit, and commercialization of guanaco products, which were only allowed if they were obtained from live animals. In this sense, the GNMP pretended to ensure conservation-oriented non-lethal management mechanisms so that the guanaco will fulfil its ecological roles, recover its cultural value and contribute to the implementation of economic alternatives compatible with habitat conservation. To achieve this, the National Plan proposed the live shearing and release of wild populations as one of the possible forms of management, while at the same time prioritizing the evaluation of its ecological sustainability, economic feasibility, and social scope (Nugent et al. 2006). Captive breeding was also accepted as a form of utilization of the species, which was based on the extraction of newborn calves from the wild to establish a breeding stock. However, the implementation of breeding stock led to high mortality of the captured newborns and young animals due to inadequate feeding and the presence of diseases (Sarasqueta 2001).

Most of the provinces where the guanaco is distributed adhered to the GNMP and, in some of them, specific legislation was drafted to regulate various aspects of its conservation and use. Due to the strong pressure from the livestock sector during the last few years, the GNMP was modified in 2019, allowing harvesting for commercial purposes, like meat, fibre, and sport hunting. This severe setback in conservation regulations for the species is aggravated by poaching, a result of the scarce institutional control capacity (for more details see Chap. 6).

Different provinces have developed unequal regulatory frameworks, reflecting the pressure exerted by different stakeholders and the diversity in the conservation status of the species throughout its distribution. This leads to regulations that are very restrictive in some provinces (higher degree of protection) and others that encourage exploitation of the species. For example, in Mendoza province, where the abundant populations of the species are limited to two protected natural areas (Laguna del Diamante Provincial Reserve and La Payunia Provincial Reserve), the only specific regulation is a Provincial Decree N°110/2007 in which the province adheres to the 2006 National Management Plan. Therefore, the authorization to implement management actions for this species is ruled by environmental norms that regulate other activities such as oil extraction. In this sense, the Decree requires the development of environmental impact assessment procedures for any project that could potentially affect the environment and, specifically, when projects involving wild guanaco management actions are proposed, not only the impact on the species is considered, but also the impact generated by the assembly of the capture structures. This procedure is very rigorous and requires the approval of different sectors, such as the environmental agency of the local municipality, the provincial Ministries of Economy and Social Development, the Office of Renewable Natural Resources, environmental NGOs, and state research institutes, among others. Thus, the authorization process for this activity is time-consuming and costly for the interested producers.

In contrast to this regulatory scenario, in Santa Cruz province, where there are abundant populations, only the presentation of a project is required, which is approved by the application authority only. This easing of regulations mostly responds to the need of the authorities to correspond the pressure from the livestock sector to limit competition between guanaco and domestic animals, facilitating the implementation of guanacos' shearing and meat harvest. As can be seen from these two opposite examples, it is still necessary to work on legislation that regulates separately different kinds of management activities, especially those that respond to extractive objectives.

After the approval of the Guanaco Management National Plan in 2006, most of the Patagonian provinces adhered to this national regulation except Río Negro and Tierra del Fuego. Particularly, provinces such as Chubut (Resolution No. 131/2012) and Santa Cruz (Decree No. 32/2015) have their own Provincial Management Plan.

7.3 Scientific Bases for the Establishment of Management Systems

Although the guanaco continues to be considered a pest by the livestock sector which maintains productive models without environmental considerations, and is persecuted across Patagonia, the high value of its fibre on the international market has modified the vision of some producers whose fields harbour relatively high densities of guanacos. Guanaco capture, shearing, and release initiatives began in the late 1990s and increased rapidly (Baldi et al. 2010). Similar growth happened in the captive management of the species. By 2009, there were already 15 ranches legally registered with guanacos in captivity and nine establishments that managed wild populations for shearing, eight on private land and one on public land. In 2011, a new management experience was added on public land. In general, the management of wild guanacos in most private farms in Patagonia has followed the logic of "invest little and earn a lot" without taking into account good practice protocols that consider the animal welfare concept. As a consequence, in many cases, the mortality rate associated with captures and shearing has been high (Carmanchahi, personal data). Provincial governments tried to regulate shearing activities through protocols for capturing and handling animals; however, the capacity to supervise management operations, information on post-capture mortality, and the consequences on the population's dynamics under management are still low.

In this section, we discuss the contributions of scientific research that allowed the establishment of management actions for the species, in a comprehensive manner and with a focus on Argentinian Patagonia. We describe and review the scientific evidence gathered in three management systems (1) Live shearing management; (2) Harvesting for meat management; and (3) Captive breeding management.

7.3.1 Live Shearing Management

In the last 20 years, diverse aspects of the effects of live shearing guanaco's management have been studied. The main contributions made by recent studies examined the response of wild guanacos to capture and shearing on physiological, behavioural, and population parameters. Below we describe the most relevant and recent data related to these aspects.

7.3.1.1 Effects of Live Shearing on Physiological and Behavioural Parameters

From a physiological perspective, animals manifest endocrinological responses as a mechanism to cope with environmental changes (Reeder and Kramer 2005). The individuals' response to immediate environmental challenges such as predation, aggression from conspecifics, food scarcity, high density, or others derived by human activities such as tourism (Creel et al. 2002) and management (Carmanchahi et al. 2011; De Nicola and Swihart 1997) is mediated by the activation of the hypothalamic–pituitary–adrenal (HPA) axis (Sapolsky et al. 2000). These challenges trigger a cascade of physiological responses that mobilize energy through mediators like catecholamines and glucocorticoids (Reeder and Kramer 2005; Sapolsky et al. 2000). Glucocorticoids (GC, cortisol, and/or corticosterone depending on the species) are adrenal steroid hormones that play an important role in maintaining homeostasis in vertebrates (Goymann and Wingfield 2004; Wingfield and Sapolsky 2003) and regulate the availability of energy by influencing gluconeogenesis, glucose use and protein metabolism (Boonstra 2005). These hormones also play a central role in the behaviour of individuals, influencing reproductive status, social behaviour, and survival (Boonstra 2005; Creel 2005; Nelson 2005; Schjolden et al. 2005). To understand how an unpredictable event, such as animal capture and restraint, impacts an individual's cortisol levels, it is necessary to know the profile of this hormone throughout the annual cycle in response to predictable natural conditions (e.g. seasonality, resource availability). This data will allow establishing if an animal goes into a state in which the disturbance induces a decreased overall health and a resultant decrease in survival and/or reproductive success. Regarding this matter, some diagnostic field studies have been done, assessing annual hormone profiles in guanacos (Ovejero et al. 2016) and the influence of diet quality on these levels (Gregorio et al. 2019). The determination of GC levels has developed into an important tool to evaluate the effects of sustainable use (capture, shearing, and release) on wild South American camelids (Arzamendia et al. 2010; Baldi et al. 2004, 2006; Carmanchahi et al. 2011; Marcoppido et al. 2017; Taraborelli et al. 2011, 2017). Researchers have been able to estimate GC levels, comparing the responses according to sex, age category, and other relevant aspects related to the management itself, such as total retention time (TRT), which is defined as the duration of roundup plus handling (capture, shearing, sample extraction, and liberation), and handling time, which referred to the period between immobilization (capture, shearing, sample extraction) and release.

One of the first studies performed found a positive correlation between TRT and serum cortisol levels, which reached a plateau after 80 min retention time, despite the persistence of the stressor agent (Carmanchahi et al. 2011). Other studies evaluated the cortisol concentrations by sex in guanacos (Table 7.1), showing that the levels in males were consistently lower than in females (Carmanchahi et al. 2011). This difference may be related to the central action of gonadal steroids (Handa et al. 1994). Higher cortisol levels in females may be related to pregnancy, a period of high energy expenditure in the life history of females (Boonstra et al. 2001), in which cortisol levels increase during late stages (Reeder and Kramer 2005). Regarding age category, there is no consensus given that Carmanchahi et al. (2011) did not find significant differences in the cortisol levels of the different age categories, while Taraborelli et al. (2017) found that cortisol levels were higher in juveniles than in adults (juveniles 32.1 ± 1.8 ng/mL, adults 28.9 ± 2 ng/mL). The high serum cortisol in 2007 and 2010 compared to the rest of the years sampled (Table 7.1)

Table 7.1 Guanaco cortisol levels in ng mL^{-1} ± s.e. (n) by sex and age categories during the handling and shearing activities carried out at La Payunia Reserve (Mendoza Province, Argentina). Cortisol concentration in the serum fraction was determined by using Immunotech 125I-Cortisol Radioimmunoassay kit (Cortisol RIA DSL-2000, Diagnostic Systems Laboratories, Inc., Webster, TX; Carmanchahi et al. 2011). The sensitivity of the assay was 3.62 ng/ml

	Cortisol ng mL^{-1} ± s.e. (n)			
	2006	2007	2009	2010
Males (all ages)	12.69 ± 1.10 (40)	34.12 ± 1.59 (48)	20.95 ± 1.35 (21)	35.13 ± 2.05 (30)
Females (all ages)	16.91 ± 1.91 (15)	44.70 ± 2.51 (15)	22.97 ± 2.34 (7)	37.37 ± 5.37 (8)
Juveniles (<2 years old)	14.47 ± 1.45 (34)	37.04 ± 1.73 (22)	25.62 ± 2.97 (19)	33.87 ± 3.18 (11)
Adults	12.84 ± 1.07 (21)	36.43 ± 2.06 (41)	20.77 ± 1.15 (5)	36.30 ± 2.43 (27)

could be a consequence of the particular weather-related conditions and primary productivity of these years (Taraborelli et al. 2017). These results highlight the importance of considering the environmental conditions in the management site throughout the entire year.

Other studies estimated cortisol and corticosterone responses to management activities (e.g. capture, handling, shearing, and release) and assessed if these steroid hormones share the same functions (Ovejero et al. 2013). While similarities would confirm the accepted view of shared physiological functions, differences would suggest that the hormones do not necessarily overlap in their roles and exhibit some differences in their functions. TRT was measured as the intensity of perturbation. This study found a higher response of cortisol than corticosterone under the same intensity of perturbation, suggesting that, under natural conditions, both hormones are affected differently by environmental stimuli or that they are subject to different endogenous regulations of their seasonal secretion.

Physiological and behavioural variables can be combined to provide insights into stress conditions in wild animals during handling. In this sense, two studies show how handling activities impact on stress behavioural responses and physiological adjustments in guanacos (Taraborelli et al. 2011, 2017). Stress behaviour was defined as the occurrence of spitting, kicking, escape attempts and vocalizations, such as snorts and sharp shouts (Arzamendia et al. 2010; Taraborelli et al. 2011; Arzamendia and Vilá 2012). The studies showed that the percentage of stress behaviour increased with the number of guanacos in the corral (Taraborelli et al. 2011) and with handling time (Taraborelli et al. 2017). However, after 15 min of being manipulated, stress behaviour rates began to decline, probably due to the animal's fatigue. In addition, handling impacted differently according to the individuals' age category: Juvenile guanacos showed higher stress behaviour rates than adults (juveniles: 3.4 ± 0.9 and adults: 2.7 ± 0.4 frequency/min) and also higher levels of serum cortisol. These results suggested that special care may be needed when manipulating young individuals.

The high rate of stress behaviour in male guanacos was related to lower cortisol levels. This negative association did not occur in female guanacos likely because dominance conflicts are only between males (Taraborelli et al. 2011). These authors proposed two possible explanations for this negative relation between stress behaviour and cortisol levels in males: (1) Captured and shorn males were exposed to acute stress that lasted up to 48 h, where the long-lasting rise in cortisol levels could have produced an effect of physical exhaustion, at which point an animal would not respond to stressors. (2) Behavioural stress responses may be a successful coping strategy to reduce the physiological stress response.

7.3.1.2 Other Physiological Parameters Related to Handling

Several studies have reported other physiological parameters measured during shearing activities, contributing to a more comprehensive understanding of the cascade of physiological events triggered during handling. For managed guanacos, heart rate (79.58 ± 2.05 beats $min^{-1} \pm$ SE) and body temperature (39.46 ± 0.13 °C $\pm$ SE) did not show significant differences between sexes, ages, or the combination of sex and age categories in either of the variables. Also, there were no significant correlations between cortisol levels and heart rate or body temperature (Carmanchahi et al. 2011). In other studies, the levels of blood urea nitrogen (BUN), creatine kinase (CK), aspartate aminotransferase (AST) and lactate dehydrogenase (LDH) were higher than reference maximum values for free-ranging and captive guanaco in 18,4% of the total animals tested (Rago et al. 2010). More recent studies assessed the relationship between CK activity and stress behaviour. They found that CK levels were more fluctuating in juveniles than in adults and that this enzyme activity was related to a higher occurrence of stress behaviour (Panebianco et al. 2017). Finally, Taraborelli et al. (2017) found that guanacos with poor body condition (see Sect. 6.3.4.1 for a description of body condition assessment) showed higher neutrophil/lymphocyte ratio (8.7 ± 5.9 N/L ratio) than individuals with better body condition (5.4 ± 0.9 N/L ratio). The high N/L ratios in guanacos with lower body condition scores could be explained because animals in poor condition are less capable of avoiding injury. This research also showed a positive relation between N/L and serum cortisol levels, in accordance with the results of Bonacic et al. (2003) in vicuñas.

The behavioural and physiological records can be used to measure stress responses. Changes in behaviour allow animals to either escape or counter challenges, while the autonomic and neuroendocrine response provides the animal with the resources needed to meet the demands of the altered behaviour, as well as maintaining homeostasis during the aversive situation (Moberg 1985). Taraborelli et al.'s (2011, 2017) findings indicate that behavioural stress responses cannot be used as a simple surrogate for glucocorticoid levels. In this regard, studies that monitor both parameters as indicators of stress during management operations are crucial. The knowledge of the endocrine state of an animal might be relevant to conserve the species, and field endocrinology can be added to the arsenal of several tools employed by conservation biologists. Additionally, endocrinology and ethology can contribute to conservation in general (Wingfield et al. 1997; McCormick and Romero 2017; Madliger et al. 2018), and the monitoring of glucocorticoid levels and stress behaviours during management may help to make informed decisions to preserve the species.

Overall, the studies analysed showed that prolonged TRT during management determines the increase in plasma cortisol levels and stress behaviours. Data collection during management events enabled continuous improvement in capture and shearing practices. This adaptive management approach allowed to make recommendations, such as avoiding the simultaneous management of a large number of animals, in order to reduce TRT, and maintaining a low number of individuals per corral to diminish stress behaviour (vocalizations and agonistic behaviour; Taraborelli et al. 2011). The results showed that shearing activities induced behavioural and physiological changes. Guanacos with poor body condition scores (<2) should not be sheared, and juvenile individuals should be handled first, with special care (Panebianco et al. 2017; Taraborelli et al. 2017). Moreover, handling time should be as short as possible, to minimize stress (Taraborelli et al. 2017). Therefore, body condition score and age should be in situ markers of the potential stress response to handling activities, a tool to decide whether an animal should be shorn or not.

7.3.1.3 Effects of Shearing Management on Populational Parameters

In addition to the behavioural and physiological effects mentioned above, scientific studies contributed to the understanding of the effect of captures for shearing of wild guanacos on population parameters (Rey et al. 2012; Carmanchahi et al. 2014). The first studies on the subject reported the demographic effects of live shearing on a guanaco population in a Patagonian sheep ranch in Río Negro Province between 2003 and 2009, based on the analysis of movements, population trends, and survival, comparing paddocks with and without roundups (Rey et al. 2012). The results showed that guanaco population trends in paddocks with and without roundups were stable in periods of average environmental conditions, but declined in years of harsh conditions (e.g. severe drought). After roundups, there was a temporary decline in densities, probably due to the altered guanaco behaviour. The annual survival rate estimated via capture-recapture was 0.82 without differences between sex and age groups. However, the authors reported that 4 out of 10 male guanacos radio-tracked after the summer roundup (e.g. February) died within the following 2 months, presumably from capture myopathy due to inadequate management. Taken together, the results of this study highlight the importance of considering the environmental conditions and the period (early spring or summer) when implementing management actions. Moreover, they suggest that if the management activity follows the strict animal welfare guidelines, live shearing activities will not imperil guanaco populations (Rey et al. 2012).

In Carmanchahi et al. (2014), survival, daily movements, and habitat use of the managed animals were analysed comparing two populations in North Patagonia: a partially migratory wild guanaco population inhabiting a protected area (La Payunia Provincial Reserve, Mendoza Province) and a sedentary population living in a sheep ranch (Río Negro Province). In this study, population variables were assessed by radio-telemetry and line-transect surveys before and after management actions. The results were similar to those found in Rey et al. (2012), indicating a high post-shearing survival rate in both populations and similar yearling production in shorn and non-shorn females in the migratory population. Regarding density and population structure, there were no significant differences in the population parameters before and after shearing in the sedentary population. In contrast, in the migratory population, animal density decreased and the population structure changed significantly after assembly of the capture structure, returning to pre-assembly levels 1 month later. The mean daily distance moved by radio-collared guanacos during the first 2 days after shearing was three times longer than during the following 30 days. There was a 25% decrease in the mean home-range size of shorn guanacos between the first and second months after shearing but this decline appeared to be associated with a seasonal change in movement because a similar reduction occurred during the same period the following year, when the guanacos were not shorn. Live-shearing modified the spatial distribution pattern in the sedentary population but did not have a significant effect on the migratory population. These results support the hypothesis that the effects of capture and shearing of wild guanacos differ in sedentary and migratory populations. The adaptive importance of migratory movements is to guarantee favourable conditions for the existence and reproduction of the population (Fryxell and Sinclair 1988). Capture and shearing of wild guanacos disturbed population parameters significantly but for a relatively short period. Specifically, dispersion and group disruption were similar to the findings of Sarno et al. (2009) for vicuñas, which could impact social composition and population dynamics if not minimized by appropriate management.

Among the recommendations that emerged from the two studies reported here, we strongly suggest to the managing authorities to not allow pre- and post-partum roundup and shearing in the same year. Although the effect of this activity on the mother-calf relationship is not known, disruption cannot be ruled out. If implemented, postpartum shearing should include the building of pens to reunite mothers and their calves before release. The addition of these recommendations to wild guanaco shearing management actions, with strong empirical support, accompanied by high animal welfare standards and continuous monitoring, are key to the sustainability of the use and the conservation of the species, as well as to the socio-economic development of the region.

In summary, human disturbance can be defined as any human activity that changes the contemporaneous behaviour or physiology of individuals (Nisbet 2000; Walker et al. 2005). Fibre harvesting in wild camelids is a kind of human disturbance that could be considered as a “Positive Management” (Nisbet 2000), since it maintains the individuals alive and helps to promote a positive perception of the guanacos due to economic incentives to livestock producers and pastoralists, which have historically considered this species as a competitor of cattle for pastures. Anthropogenic disturbances can be evaluated through the assessment of behavioural and physiological consequences. An animal appearing to be calm may in fact be experiencing high physiological costs in response to the disruption (Walker et al. 2005). Therefore, the physiological evaluation of the individuals subjected to the disturbance can demonstrate the real state of the animal. Fibre harvesting is an unpredictable event and requires responses on a facultative basis (McEwen and Wingfield 2003; Wingfield 2004). The outcomes of the recent research mentioned here, incorporated into animal welfare protocols, have reduced the mortality and stress associated with shearing management and thus the impact of live-shearing activities on population structure and fitness.

7.3.2 Management for Meat Production

Guanaco harvest models emerged as a response to strong pressure from some groups of farmers in Patagonia with increasing guanaco populations in their properties. In this sense, the government of Chubut Province (Argentina) commissioned some researchers (Rabinovich and Zubillaga 2011a, b, 2012) to develop a viable model for controlling population abundance, generating a product not commercially permitted by the GNMP up to that time: the meat of guanaco.

These models require an estimate of population density and abundance with a long time series. Since this information did not exist for Chubut province, the model was developed using a database of a population inhabiting a ranch in the Chilean portion of Tierra del Fuego Island (Zubillaga et al. 2014, 2017, 2018), approximately 1600 Km to the south. The parameters estimated in Tierra del Fuego were compared with data available from three ranches of Chubut that were considered for a harvesting pilot experience. Differences were found among study sites, principally in primary productivity that was estimated using the precipitation regime. One of the main problems of this kind of estimation in Patagonia is the variation in precipitation, even in small areas, and the scarcity of weather stations to document that information correctly. For this reason, vegetation indexes like the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI) are preferred to estimate primary productivity, as used by several authors concerning guanaco ecology (Pedrana et al. 2010; Schroeder et al. 2014; Marino et al. 2014; Travaini et al. 2015).

The area occupied by guanacos in Chubut province is generally shared with sheep (Baldi et al. 2001; Pedrana et al. 2010; Travaini et al. 2015; Antún and Baldi 2020. See Chap. 3). For this reason, the estimates of carrying capacity, a parameter of utmost importance for the development of harvest models, must consider the presence of both herbivores (Rabinovich and Zubillaga 2012). To do this, an equivalence between guanaco and sheep was established, which states that 1 guanaco = 1.5 sheep. This conversion was called guanaco units, and all the herbivores were transformed into these units (Rabinovich and Zubillaga 2011b). Afterwards, the number of sheep in each ranch was considered, and the carrying capacity for guanacos was estimated as a subtraction, calculating what remains available after cattle use of the resources (Rabinovich and Zubillaga 2012). For example, if the carrying capacity of a specific area is 13 guanacos/Km^2, and sheep density is equivalent to 10.6 guanacos/km^2, the carrying capacity for guanacos is 2.4 guanacos/km^2. Consequently, if guanaco density increases, those animals are above the carrying capacity of that area (Rabinovich and Zubillaga 2011b).

Estimating the carrying capacity of two notoriously different herbivores is challenging and should not be oversimplified. Guanacos coevolved with different South American environments and are highly adapted to different habitats; their diet includes trees, shrubs, grasses, herbs, lichens, epiphytes, and cacti (Raedeke 1979; Bahamonde et al. 1986; Puig 1995; Puig et al. 1997; Baldi et al. 2004). With the structure and shape of their cleft lips and teeth, they are highly selective about the parts of the consumed plants. They cut instead of pluck, allowing early regrowth, and avoiding high impact on soil and vegetation (Vilá 1999). Also, guanacos can use degraded habitats with low primary productivity where sheep are absent (Pedrana et al. 2010; Travaini et al. 2015; Marino et al. 2020). Furthermore, the efficiency of the species in incorporating nutrients from forage should not be ignored. Experimental studies compared dry matter intake (in terms of metabolic live weight) in guanaco and sheep and found that guanaco intake is significantly lower than sheep intake. So, guanacos have higher digestibility of dry matter, neutral detergent fibre, and acid detergent fibre than sheep. Then, for assessing stocking rates, equivalence should be considered 1:1 (Moseley 1993).

To recommend the number of individuals to be harvested, the proportional threshold harvesting rule was proposed, which consists of establishing a threshold under which animal hunts are not allowed (Lande et al. 1997). There are different ways to achieve it, some of them maximize the average of animals extracted, and others maximize the population growth rate. After evaluating different criteria and the internal variability among different ranches, the authors decided that the extraction threshold should be evaluated in each ranch. Threshold values were proposed for each place where the pilot experiences were going to happen (Rabinovich and Zubillaga 2012).

As it was stated before, the harvesting model described was requested by Chubut province, but it was never applied there. In 2017, the model was adapted for Santa Cruz province (Rabinovich 2017a, b). In this revised model, the concept of carrying capacity was changed by stocking density which is calculated in sheep equivalents instead of guanaco equivalents, but the conversion is the same as mentioned above. This model was presented as a user manual whose purpose is to calculate, in a simple manner, the recommended number of animals to extract. In this manual, the parameters of the model (guanacos' density, stocking density, safeguard factor to preserve guanaco population) are estimated by the user, instead of being calculated by the model (Rabinovich 2017b). For example, to estimate stocking density, the user does not complete the primary productivity of that specific ranch; instead, carrying capacity should be estimated outside the model, and then the data filled in the software. Estimation of this parameter is a topic of concern since there is no agreement about the best way of calculating it in the scientific local community, even for cattle (Golluscio et al. 2009). If stocking density is estimated using different approaches, this might be risky for guanacos' conservation. Some research considers that one guanaco is equal to two sheep (Von Thüngen and Bay Gavuzzo 2014), which leaves less space for guanacos in each ranch if we follow the terms of the harvesting model. Therefore, there is no guarantee that the users of the model will apply the original rule (1 guanaco = 1.5 sheep), which is also arbitrary, but at least more conservative than other criteria discussed in the scientific community. As a consequence, the absence of a unified criterion for these estimates might lead to overexploitation of the guanacos' population.

Some ranchers of Santa Cruz province might perceive an increase in guanaco population, but there is no evidence about that at a regional scale, and only predial surveys are available. Possibly, the perception of population growth is due to the reoccupation by guanacos of the empty areas that were left after livestock production ceased; since guanacos can consume low-quality forages and inhabit degraded areas that can no longer sustain sheep production (Marino et al. 2020; Pedrana et al. 2010; Travaini et al. 2015. See Chap. 3). As a consequence, more information is necessary to decide the actual status of the populations and whether it is possible to harvest individuals or not.

Additionally, the importance of a solid harvest regulation is needed to minimize population risk (Fryxell et al. 2010) and the importance of periodic population monitoring to make good harvesting decisions. Guanaco meat production and exportation were promoted by the Argentinian government (SAyDS 2019). To date, there are no public reports of guanaco's meat sale outside the country, the number of guanacos harvested, or population surveys in the areas where harvesting was done. Even so, guanacos are not an attractive species for game hunting, and the main reason to hunt the species is the desire to reduce guanacos' density to introduce more sheep in the areas, but since they are already overgrazed, this is not a solution (Marino et al. 2020; Oliva et al. 2016).

There is no evidence that guanaco populations endanger the integrity of pastures or livestock production (see Chap. 3). Even if a significant number of guanacos were harvested from the Patagonian grasslands, factors driving land degradation and production losses (i.e. heterogeneity of grazing and excessive stocks) will continue operating, unless traditional land management practices are modified (Marino et al. 2020). Oversimplification of grassland systems degradation may lead to dramatic consequences for guanaco conservation and for the whole preservation of the Patagonian environments.

7.3.3 Captive Management

In the 1990s, some Patagonian producers became very interested in breeding guanacos in captivity, being motivated and advised by the National Institute for Agricultural Technology (INTA). This type of management, approved in the GNPM, can be carried out intensively, with large numbers of animals kept in small spaces with supplementary feeding, or extensively, in which guanacos are kept in large areas fenced with wire, under conditions similar to those used for sheep. In most cases, the initial stock to start the activity comes from the wild, capturing 3- to 10-day-old calves, which are artificially fed with powdered cow's milk (Defosse et al. 1981; Sarasqueta 2001). There are few technical reports on research supporting the definition of management procedures (Defosse et al. 1981; Amaya and Von Thüngen 2001, 2003; Sarasqueta 2001). These reports provide practical information on how to carry out the breeding and maintenance of individuals without clarifying the existence of scientific studies to support such management decisions. This technology was used in different ranches located in the provinces of Neuquén, Chubut, Río Negro, and Santa Cruz (Amaya and Von Thüngen 2001; Lichtenstein 2013).

Captive management still faces some challenges, such as determining technical feasibility; defining the scope concerning the conservation of the species, and evaluating if this management modality offers economic benefits to the producer. Existing reports mention several health problems that cause mortality of individuals during the first months of life. These mortalities are mainly associated with the capture stress and the change in diet (from mother's milk to artificial feeding), which produce severe diarrhoea, leading to dehydration and death of the calves recently collected from the wild (Sarasqueta 2001). Reports of mortality in captive guanaco offspring indicate that 88.8% of the offspring died, and the clinical symptoms and findings during necropsies were consistent with enterotoxaemia (a disease caused by toxins from intestinal Clostridium bacteria causing severe lung and brain damage (Larrieu et al. 1987). Other diseases also require close attention and sanitary treatment, such as mange, sarcosporidiosis, skin mycosis, conjunctivitis, and salivary gland disorders (Sarasqueta 2001). In addition, since guanacos are gregarious and maintain social behaviours, their handling could generate risky behaviours for the operators and confrontations and injuries between individuals.

Captive breeding was also carried out in Chilean Patagonia (González et al. 2000; Bas and González 2000). Although it was observed that it could be a potential economic activity, like in the Argentine experiences, some difficulties were identified, such as the complexity in capturing wild offspring to start the breeding stock, the lack of knowledge for the management of artificially breastfed offspring, high mortality rates during the first year of life, difficulty in designing adequate facilities and a management routine (Bas and González 2000). The Chilean experience recommends selecting reproductive males and castration to reduce the aggressive behaviour of individuals. In addition, it is suggested that management should focus on socializing the guanaco with humans, so that individuals are habituated to their presence (González et al. 2000; Bas and González 2000). A certain level of habituation can be achieved through artificial nursing, regular training through eye contact and handling, and frequent handling associated with feeding (Bas and González 2000).

The economic and biological impact of captive breeding was also studied for vicuñas. Most studies show that the economic benefits of this management system are, at best, unproven (McNeill and Lichtenstein 2003). Vicuña captive management proved not to have the capacity or scope to conserve wild vicuña populations outside corrals, to change local people's attitudes towards vicuña conservation, or to enhance the livelihoods of poor local people. Captive management was found to disrupt the natural social organization of vicuñas and inhibit the genetic flow between populations. Other genetic consequences included inbreeding, genetic drift, and artificial selection (Vilá and Lichtenstein 2006). As in the case of vicuña, managing guanacos in captivity leads to a loss of the ecological role of this species within the ecosystem as it no longer fulfils its functions as prey and consumer of vegetation. It also leads to artificial selection, as docile behaviour is selected and the administration of drugs leads to unnatural survival rates and speciation processes. These characteristics call into question the contribution of this approach to the conservation of the species.

7.3.4 Protocols for Good Management Practices

7.3.4.1 Animal Welfare Criteria for Wild Guanaco Management

Animal welfare (AW) is defined as the consideration of the animal in a state of harmony with its environment and the way it reacts to environmental problems, taking into account its comfort, housing, treatment, care, nutrition, disease prevention, responsible care, handling, and humane euthanasia when appropriate (Zinsstag and Weiss 2001; Nielsen and Bergfeld 2003; Underwood 2002). Working within a framework of AW has not only ethical but also commercial connotations. The generation of products with good practice certification could have greater competitiveness, access to elite markets, and higher prices in international markets.

At present, animal welfare concerning the sustainable use of wild animals is a dynamic field point. Animal welfare issues were omitted in cases of in situ shearing of South American camelids for a long time. In 1997, the first research on the possible consequences of wild guanaco capture and shearing activities began to be carried out. In these studies, the authors concluded that research was still needed on the consequences of capture and shearing associated with stressful situations in South American camelids and their importance in conservation (Bonacic 2000; Goddard et al. 2003). As stated in the previous sections of this chapter, recent research in guanacos has suggested that although there are physiological effects manifested by an increase in serum cortisol levels, these would not be of such a magnitude as to put life at risk (Carmanchahi et al. 2011; Ovejero et al. 2013; Taraborelli et al. 2011, 2017). Studies on the influence of management on mortality, density, and social structure of these camelids indicate modifications in the parameters studied, although they would not be of a permanent nature (see Sect. 7.3.1). Altogether, these results suggest that, with proper animal management, this activity could be feasible within a sustainable framework.

The sustainable use of wildlife emphasizes population viability, conservation of the environment, and the economic benefits derived from its use. The successful use of wildlife should include research on the subject, accompanied by professional ethics and the implementation of good practices and adaptive management, framed in updated legislation under the supervision of the competent authorities. The first set of guidelines linked to animal welfare related to guanaco management practices derived from the experience of the authors who began working in shearing activities in the year 2000. These guidelines were prepared for the first Guanaco National Management Plan in Argentina, implemented in 2006 (Baldi et al. 2006). Then, the scientific research described in the previous section was used to adjust and improve management actions to ensure AW and was incorporated in updates published in specific protocols during 2012 and 2017 (Carmanchahi and Marull 2012, 2017).

The protocol contains animal welfare criteria for wild guanaco management on the following topics:

Authorized Periods Shearing activities in Patagonia can be authorized in two periods, before or after the calving season. Although both periods have advantages and disadvantages, pre-calving shearing is recommended because the risk of trauma and calf mortality is low and the probability of separation and disruption of mothers and calves is reduced. It also allows the animal to regrow its hair to face the winter.

Roundup The protocol lists a series of recommendations related to roundup methods, speed, time of day, and duration. These include short roundups with horses during the morning, avoiding high temperatures, and always prioritizing the safety of the animals (Fig. 7.1a). It is essential that herding is carried out carefully and by trained personnel, leading the animals to the capture infrastructure without forcing them to move faster than their normal walking pace.

Enclosure and Passage Through the Holding Pen The corral trap has two V-shaped arms, one pre-capture corral, a capture corral, three successive corrals, a holding pen, and a shearing corral (Fig. 7.2). Regarding the infrastructure for capture and handling of the animals, the protocol recommends using soft materials (e.g. nets, shade nets, wires, carpets) to reduce the trauma or death of the animals caused by impacts inside the enclosures. It also suggests that the pens are subdivided by wooden doors (successive corrals) to facilitate animal handling and work with small groups of animals, avoiding overcrowding, a strong stressor for the captured animals (Taraborelli et al. 2011). Reducing the view out of the pens by placing carpets to minimize stress is also recommended (Figs. 7.1b and 7.2).

The holding pen should be constructed of wooden panels or similar material, with no sharp edges and the absence of gaps where animals could introduce their limbs. The roof should be covered with shade nets or similar material to reduce escape attempts and possible injuries when jumping.

Restraint and Immobilization To immobilize the individuals in the holding pen, each guanaco should be restrained, blindfolded, and placed on a wood stretcher by two to three people. Ear restraint should be avoided as this type of manoeuvre results in immobilization but as a result of painful stimuli which increases stress. One operator should hold the head during the complete activity (Fig. 7.1c). Once on

Fig. 7.1 Stages of wild guanaco live shearing. (**a**) The guanacos are herded on horseback and led to the corrals. (**b**) The successive corrals have walls covered with a carpet that reduces the external visual stimuli. These structures allow animals to be divided into smaller groups, avoiding crowding and facilitating management. (**c**) Each guanaco is immobilized, blindfolded, and placed on a wood stretcher, where trained personnel shear the animal using an electric sheep shearing machine. Each shorn guanaco is identified with a collar and numbered tag. (**d**) After shearing, operators take the guanaco to the liberation site with the hood in place. (**e**)The liberation consists of an open place, outside the shearing shed, with no obstacles to the animal's free escape. Photo credits: Antonella Panebianco (**a** & **e**); Ramiro Ovejero (**b**); Pablo Gregorio (**c** & **d**)

the stretcher, a veterinary or trained personnel should assess the body condition score, which is estimated by palpating the degree of sharpness of spinous processes, muscle mass, and fat cover adjacent to the lumbar vertebrae (Audige et al. 1998). This variable is routinely estimated during management and results in a good esti-

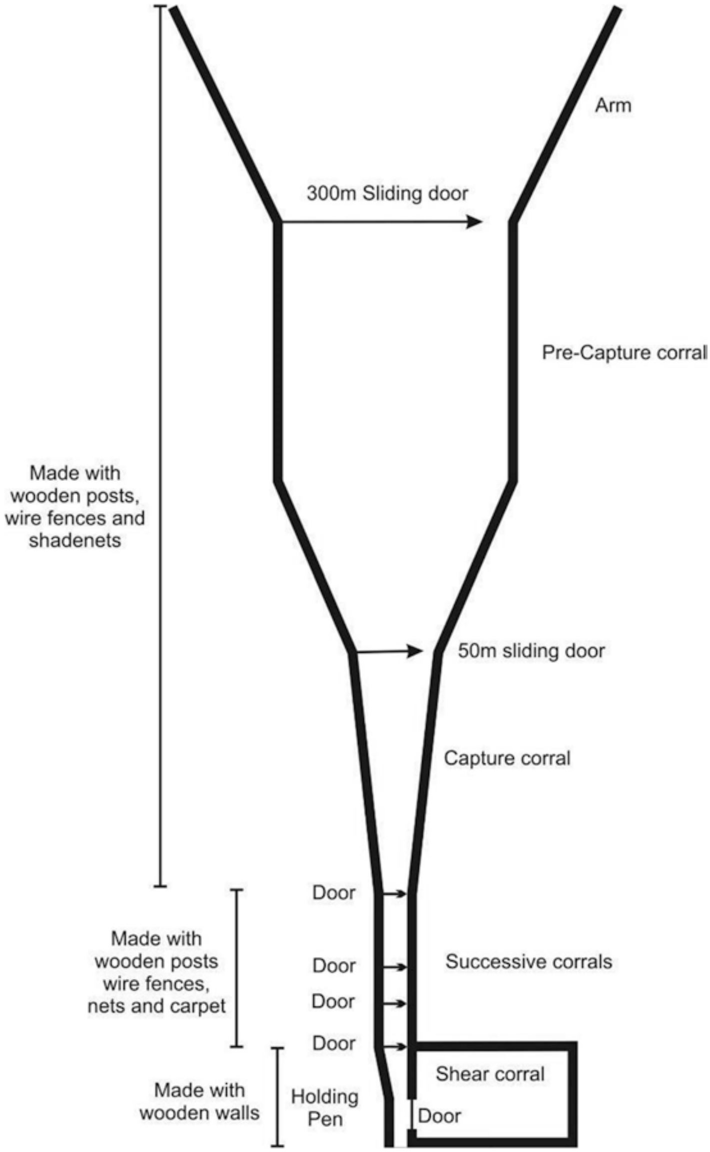

Fig. 7.2 Schematic design of the capture structure employed for the management of wild guanacos. (Reproduced from Carmanchahi et al. (2011) with permission from CSIRO Publishing)

mator of the guanaco's general state. Scores range from 1 to 5: Score 1 = Very poor condition (cachexia), Score 2 = Poor condition (emaciated or leanness); Score 3 = Moderate/normal condition (slim); Score 4 = Good condition (normal) and Score 5 = Very good condition (fat). Guanacos with poor body condition scores (1 or 2) should not be sheared.

Live Shearing The protocol recommends that the complete restraint-shearing-release procedure should be performed in the shortest time possible and suggests that the complete handling time should not exceed 10 min, as longer times may increase the frequency of stress behaviours and cortisol levels (see Sect. 7.3.1). If biological samples are taken from the captured animals, the collection process should not exceed 3 additional minutes.

It is recommended to partially shear the brown area and the white upper flanks (Fig. 7.3). It is not advisable to shear legs, neck, tail, and belly as it increases the retention time of the animal and therefore, stress. In addition, the fibre obtained from these areas has no commercial value. Moreover, it has been shown that the axillary regions and lower flanks are "thermal windows" that are regulated by different postures to reduce heat loss by radiation and convection (de Lamo et al. 1998). Therefore, shearing the ventral region and lower flanks could increase the area of these thermal windows, preventing the animals from being able to thermoregulate effectively.

Biological Sampling In case of conducting research (sanitary, physiological, genetic, etc.) that requires sample collection of different types, the protocol recommends that samples be taken by experienced veterinarians, biologists, or trained personnel. In the case of blood samples, extraction from the femoral vein is recommended.

Identification Regarding identification, wild guanacos that have been captured and sheared should be identified so they can be recognized during post-shearing surveys to assess the animals' responses to management. Collars made of durable materials (e.g., nylon) can be used, with a numbered tag attached to it (Fig. 7.1c). The use of

Fig. 7.3 Part of the guanacos recommended for shearing. Photo credit: Julie Maher

plastic ear tags is not advisable, because ears have an important role in the behaviour and communication of this species.

Retention Time Retention time is positively correlated with serum cortisol levels and stress behaviours, so the protocol recommends keeping it to a minimum. Juvenile individuals should be handled first, with special care, considering they have a higher frequency of stress behaviour (see Sect. 7.3.1).

Release When releasing the shorn animal, it should be led to the liberation site with the hood in place and the head held by an operator. Then the leashes and hood should be removed while still holding the animal by the head, giving it a few minutes to get used to the light again. The liberation should be done in an open place, outside the shearing shed, with no obstacles to the animal's free escape (Fig. 7.1d, e).

Training of Personnel Involved in the Management Before handling guanacos, personnel should be trained on roundup methods, restraint, shearing, and release manoeuvres due to the susceptibility of guanacos to stressful situations.

Population Monitoring Before and after shearing activities, the protocol recommends conducting population surveys to estimate the impact of management activities on wild guanaco populations and thus determine whether they should be carried out or cancelled.

7.3.4.2 Animal Welfare Concerns in Other Guanaco Management Systems: Meat Harvesting and Captive Breeding

The AW protocols for captive breeding systems are incomplete and, in particular in the meat harvesting system, there are no scientifically based contributions that have allowed the development of AW protocols. The lack of AW protocols for meat harvesting could be because it is a recent activity in Argentina, and although harvesting was authorized by the competent authority, many of its aspects are still in an experimental phase.

Regarding guanaco meat production, the 2019 GNMP briefly outlines the harvest period and specifies that good practice protocols should be applied during herding and shearing, using the manual written by Carmanchahi and Marull (2017) for live shearing experiences and the Operative Plan (2018) as references. The GNMP determines that only adult and juvenile animals over 1 year of age will be slaughtered. It also recommends that females captured after 15 September should not be slaughtered and must be released, but this recommendation is sometimes not taken into account, as operations have been carried out outside this period. For example, in the case of the operations done in the Project for the Sustainable Use of Wild Guanacos, organized by the National State, the government of Santa Cruz province, and private producers, 687 animals were slaughtered between 20 September and 8 October (Final Report. Proyecto Estratégico Uso Integral y Sustentable del Guanaco

Silvestre. 2019). At the beginning of this activity, the animals were slaughtered in the field, but later the live animals began to be transferred to the slaughterhouses, which requires the development of new AW protocols absent in the current GNMP. The GNMP only identifies a procedure, which is summarized in the following steps:

– Step 1: desensitization (using less cruel methodology), throat slitting, evisceration, and transfer by refrigerated truck from field to slaughterhouse. To avoid the criticism that obtaining and marketing fibre from dead guanacos could cause, the local enforcement authority authorized producers to shear the animals alive and then slaughter them. This gives producers the possibility to sell the fibre as coming from live animals.
– Step 2: separation of carcass and pelts.
– Step 3: deboning, packaging, and freezing (−25 °C).
– Step 4: cold storage (−18 °C).
– Step 5: commercialization and trading, with the corresponding authorizations by the provincial wildlife application authority.

About the step of desensitization and slaughter, both critical steps for AW, the GNMP mentions that the assistance of a veterinary professional under the orders of the enforcement authorities must be provided (this does not always happen). In addition, specific key actions must be carried out: a control of the capture infrastructure; the personnel will facilitate the immobilization of the animal for its correct desensitization; and ante-mortem inspection in accordance with the guidelines described in Decree 4238/68 SENASA (State Agency of the National Service of Health and Food Quality). During the ante-mortem inspection, the fitness of the animal to be slaughtered must be decided, in this case the physical condition must be assessed. Sometimes this assessment fails, and, for example, during the 2018 slaughter activities, 153 (22,2%) guanacos had to be decommissioned among other causes due to cachexia and injuries (Final Report. Proyecto Estratégico Uso Integral y Sustentable del Guanaco Silvestre. 2019).

Regarding the slaughter of animals, the GNMP provides some basic actions. The animal will be desensitized in order to reduce the animal's suffering to a minimum, using a Jarvis-type gun or another less cruel method. If certain symptoms are detected (rhythmic breathing, vocalizations, eye reflexes, etc.), a new shot of the desensitization method will be applied. This Management Plan states that there must be zero tolerance for the slaughter of awake animals without prior desensitization. Once the animal has been desensitized, it is raised on a metal structure on which it must be hung upright and its head must be loose. The animal's throat is then slit and it is bled.

For the sub-process of obtaining meat, the inspection of the basic infrastructure is the responsibility of personnel authorized by SENASA (National Service of Health and Agri-Food Quality), who must inspect the infrastructure elements implemented for these processes and their adaptation for the slaughter of camelids. The provincial wildlife enforcement authority must monitor compliance with the conditions expressed in the authorization for harvesting in accordance with the Guidelines and Requirements for Harvesting Projects of GNMP as well as the correct application of the Protocol of Good Management Practices for Wild Guanacos (Carmanchahi and Marull 2017).

The 2019 GNMP provided a general framework of recommendations and procedures, where it is then necessary to develop specific protocols for each province interested in carrying out actions to harvest meat from wild guanaco populations. Although Chubut's provincial guanaco management plan (2012) mentions objectives associated with the development of AW protocols, there is little content on this issue. The objectives presented there are associated with management modalities for meat utilization, captive breeding, and animal shearing, in a general framework. In the case of Santa Cruz, the province has a Guanaco Provincial Management Plan (2014). In its original formulation, it outlines the main criteria for the sustainable use of the species. However, this document lacks standards and protocols related to AW.

In relation to AW in guanaco captive breeding initiatives, there is some evidence reported from private enterprises in Chile. Bas and González (2000) mention aspects associated with the facilities (see above in this chapter, on captive breeding systems) and refer to the consideration of the behavioural traits of the animals. Captive guanacos exhibit aggressive behaviours similar to those of free-ranging guanacos (Wilson and Franklin 1985). However, the frequency of the main type of aggressive behaviours is modified with more frequent and longer fights in captivity. This has implications of adaptive value in the wild since it is the way in which territorial dominance is established and is directly related to the reproductive fitness of the animals. But it has negative implications for captive management in confined spaces and increases the risk of injuries, accidents, and stress in male guanacos. In general, the results of the behavioural work indicate that there is an effect of captivity due to the reduced space and the lack of a maternal figure during rearing. The expression of age-appropriate behaviours does not seem to be affected, but rather their duration, frequency, and dynamics of expression.

Currently, the aspects associated with AW in captive breeding and harvest management systems show key gaps in information, where there is a clear need to plan and carry out scientifically based studies that allow for the development of adequate protocols. The development of this type of protocol will undoubtedly allow the optimization of these management actions, ensuring their sustainability.

7.4 Economic Analysis

Movements in Latin America that promoted environmentally and socio-culturally sustainable production systems used basic ecological principles to study, design and manage these systems; so that they are productive, conserve natural resources, as well as are culturally sensitive, socially just, and economically viable (Altieri 2002). In this context, the sustainability of a natural resource management system requires: to be productive, stable, adaptable, reliable, and resilient; to distribute their costs and benefits equitably; and to generate processes of self-management and autonomy among the beneficiaries (Masera et al. 1999).

The environmental services provided by biodiversity, and natural resources in general, are not assigned a market price, which can be interpreted as not having a value (Villareal and Longo 2003). Assigning an economic value to these goods and services allows establishing monetary comparisons between different activities that make use of these resources, and also, determining the costs and benefits of conservation and the implicit costs of their deterioration, depletion, or extinction (Villareal and Longo 2003). However, adequate knowledge of various factors, whether biological, social, or cultural, is necessary to establish the real economic value of the resource and ensure the sustainability of its use (Tomasini 2001). On the other hand, some authors consider that the saturation of the environmental discourse with economic and financial terms is in line with the ideological and institutional construction of the dominant economic model, which sees environmental issues no longer as a sign of the crisis of capitalism, but as a new frontier for the accumulation of financial capital, giving it an advantage in reaching decision-making circles and influencing public policy (Durand 2014). There is a difficult balance between assigning economic value to natural resources and turning them into commodities.

Sustainable wildlife management requires reconciling the economic profitability of human activities with the long-term conservation of biodiversity (Hernández-Silva et al. 2018). Guanaco management programs have the same underlying logic as community-based natural resource management initiatives. The rationale is that by allowing the commercialization of fibre obtained from live-shorn individuals, the development of positive local attitudes towards conservation would be encouraged. In turn, this should result in some or all of the following: a decrease in poaching; an increase in tolerance to the presence of guanacos on private lands; better management of total grazing pressure; reduced land degradation; improved vegetation and biodiversity outcomes; and, greater support for conservation measures (Lichtenstein 2011). The hope is that rather than continue to be antagonistic towards guanacos, producers would assist government efforts in monitoring and protecting the species. Getting local people involved in conservation is the only viable option to decrease conflict with domestic livestock and to effectively manage the vast areas inhabited by this species.

Economic analyses of the different guanaco management systems (in captive or wild animals) and in different socio-productive contexts are very scarce. This lack of studies added to the lack of a transparent market determines that, in many cases, producers do not have the necessary information to decide to start management activities for commercial purposes. In this section, we present the costs associated with management, both in captivity and in the wild, as well as the main results of studies related to economic evaluations of fibre production. We also describe the commercial circuit of the fibre and some considerations about the fibre market. Finally, we analyse the commercial production of guanaco meat and discuss the contribution of this activity as a conservation strategy for the species and the economic benefits for producers.

7.4.1 Captive Management

Captive management of guanacos began in 1997 with the creation of breeding stock in Chubut and Río Negro provinces. These projects, which were approved by the competent authorities, served to unblock the restriction on Argentina's fibre exports (see Sect. 6.2 and Chap. 5). In 1999, the first permit granted by Río Negro province was obtained to shear the first 300 captive animals, obtaining 144 Kg of raw fibre sold at U$S 111/Kg (Mellado 2003). This activity was promoted in the general media, proposing the guanaco as the "gold of Patagonia" (Mellado 2003) or as the "animal that could save Patagonia" (BBC News 2012). The strong impulse given to the activity quickly obtained results and by 2003, only in Río Negro province, there were 9 ranches authorized by the provincial wildlife authority, which produced about 500 Kg of fibre that was sold at U$S 150/Kg (Mellado 2003; Lichtenstein 2013).

The promotion of this activity, even by technical agencies of the National State (Amaya and Von Thüngen 2001; Sarasqueta 2001), was not supported by economic studies. The few analyses that were carried out after the installation of ranches showed that, due to the cost of infrastructure, this activity was not economically viable and did not make significant contributions to the conservation of the species (Guirola et al. 2009; Antiman et al. 2011). The evaluation of captive breeding as a production alternative in Chubut province showed that the analysis of three critical variables (sales price, fixed labour cost, and exchange rate) determined the economic infeasibility of the activity and, therefore, the recommendation not to invest in it (Antiman et al. 2011). These results questioned the State's promotion of an unprofitable activity for the producer and whether the business was based on the sale of technology rather than on production itself.

7.4.2 Live Shearing Management

Attempts to capture, shear, and release wild guanacos started in the late 1990s and have been increasing rapidly since 2002, in particular in northern Patagonia (Baldi et al. 2010). The animals are herded mainly on horseback or occasionally on motorcycles into a trap, shorn, and released (Fig. 7.2; Carmanchahi et al. 2011). Since 2002, the capture, shearing and release of guanacos to sell their fibre increased in Argentinian Patagonia, with thousands of guanacos shorn every year and the fibre exported, mainly without added value. Between 2003 and 2016, around 40,000 guanacos were captured and shorn at 12 ranches in Rio Negro and Neuquén provinces, and a provincial reserve in Mendoza province.

Most of the initiatives for live shearing and release of guanacos are combined with traditional sheep ranching. Guanaco management is carried out in an average of 18% of the area of these ranches, while an average of 75% of the area of the ranch is dedicated to sheep farming (Baldi et al. 2010). In addition to the sheep ranches, a cooperative of herders that live in the vicinity of La Payunia provincial reserve in

Mendoza province initiated capture and shearing of guanacos in public lands inside of the reserve in 2005. La Payunia reserve harbours the largest protected population of guanacos in the species range (over 26,000 individuals, Schroeder 2013), where conflicts over land use had escalated in recent years due to the recovery of the guanaco population and because about half of the 650,000-hectare reserve is occupied by goat and cattle herders and small-scale ranchers. The provincial government considered the project of the Payun Matru cooperative as an attempt to increase tolerance towards guanacos and also provide an economic alternative to alleviate poverty in the area. In addition, to developing innovative capture and shearing methods that promote animal welfare, the cooperative is currently experimenting with producing yarn locally and exporting it (Lichtenstein and Carmanchahi 2012).

The high prices paid (or promised) for guanaco fibre until 2006 (between US$ 150 and US$ 200 per kilo), along with low prices for sheep wool, were an incentive for many producers to join the activity. The costs of starting to manage wild populations depend on the particular conditions of each farm. For example, on sheep ranches, the necessary machinery for shearing is available, so the cost is lower. The cost can be further reduced if there are sheep management structures that can be adapted to capture guanacos, such as sheds and fences, and permanent staff on the ranch.

Guirola et al. (2009) developed an economic study to understand the cost structure of the guanaco fibre production industry by surveying the costs of several ranchers that carried out shearing activities. This study was based on a series of assumptions about the shearing season that represent the highest level of the cost spectrum obtained from the ranchers and is therefore a fairly conservative model. It does not take into account the opportunity cost of raising sheep or information on tax charges. Based on these assumptions (one of which is that 1000 guanacos are sheared per season), total costs per kilogram of raw fibre produced were about US$ 45, of which US$25 were variable costs and US$20 were fixed costs. Fixed costs were reduced as they can be apportioned over a larger volume of production. Costs reach US$130 when only 200 guanacos are shorn per year, but drop rapidly to $65 if 500 guanacos are shorn per year. As a result, the producer's profitability depends not only on the variable costs and the price of fibre but also on the size of the operation. In this sense, this analysis proposes that to achieve 30% profitability, the rancher needs to shear 1550 guanacos if the price per kilo of raw fibre is US$50, while only 600 guanacos are needed if the price is US$75. At US$100/Kg, only 400 guanacos are required for 30% profit. These costs set the minimum price the rancher has to charge per kilogram of fibre.

After 2006, the situation changed dramatically: the trading companies showed less interest in guanaco fibre and started offering only US$60–80 per kilo (Lichtenstein 2013). Most of the guanaco management projects suspended their operations because of the uncertainty of obtaining a good price for their fibre and resumed prioritizing the more reliable sheep ranching. By 2010, most of the ranches had stopped operating due to the difficulty in marketing guanaco, the decrease in the price of guanaco fibre, and an increase in the price of sheep wool. The few projects that remain have begun to seek ways to add value to the fibre at a local level and find new markets (Lichtenstein 2013).

7.5 Market and Commercialization

For several decades, the wool sector in Argentina has been going through a delicate situation due to several high-impact factors, such as the sustained fall in demand for products, the increase in the cost of services associated with production, tax burdens, and the import of competing products. In this sense, guanaco fibre is not an exception to this situation, since, being a high value product, it has a high propensity to be substituted by lower value products, both from the local and international markets.

Although this species was recognized as an opportunity for the economic development of the region (FAO 1992), there have been projects in the Argentine legislature attempting to promote guanacos as a livestock, or as a harmful species (Proyecto de Ley N° 1406-D-2008, Proyecto de Ley N° S-930/2021, Resolución N° 109/2012 of the Deputies of the Province of Santa Cruz), which represents a major threat to guanaco conservation (for more details see Chap. 6). These regulations, which advance the reduction of the guanaco population, are a huge non-strategic mistake as they go against all global trends and generate a negative image when it comes to positioning guanaco fibre in the world of luxury fibres. In this sense, the definition of positioning strategies based on environmentally friendly projects will be very difficult to achieve if sustainable fibre production coexists with the business of meat and fibre from large-scale slaughtering, as is currently being planned and authorized in Argentina. To prevent this, it will be necessary to align efforts between public and private organizations to promote the positioning and use of guanaco fibre as a long-term strategic plan.

7.5.1 Fibre Market

Guanacos have a double coat fleece similar to that of cashmere. The undercoat, which is referred to as the down hair, is a fine fibre that ranges in colour from brown to dark cinnamon. The outer coast consists of coarse fibres called guard hairs which are a darker brown and help to keep debris and moisture out. Fleece refers to the whole pelage of the animal including the down hair and guard hairs, and its weight reaches 300–700 g per individual (Quispe et al. 2009). Diameter is a key factor in determining the economic value of the fibre and in adult guanacos can range between 14 and 17 μm. Another important physical parameter is the length because the longer the fibre, the finer it can be spun. Guanaco fibre has an average length of about 3 cm, which is at the shorter end of the animal fibre length spectrum (Quispe et al.

2009). Guanaco fibre is on average not as fine as vicuña but is otherwise quite similar in its thermal properties, softness, and colour.

The following links make up the guanaco fibre value chain: raw fibre, washed fibre, dehaired fibre, top production, and finally spinning as a step before the design and manufacture of final products (Fig. 7.4). The lack of information regarding the price in each of the above-mentioned links in different enterprises is a major impediment to having a comprehensive view of the guanaco fibre value chain and its market conditions. This puts producers in a weak position to negotiate the price of the fibre, as they have to deal with a few large global buyers. They also strengthen their bargaining power because they have an associated network of luxury clothing manufacturers and greater access to different quality fibres that could substitute guanaco fibre, such as cashmere. This inequality is aggravated by legislation that is often bureaucratic and centralized.

Guanaco fibre is sold by individual ranchers to either one of two trading companies with a long history in Patagonia of exporting natural fibres. These companies also buy sheep wool from the same producers and thus have well-established contacts. The companies export guanaco and vicuña fibres, mainly to Italy, where it is processed into finished goods. There is no formal market for guanaco fibre and, unlike merino wool or cashmere, there are no reference prices (Lichtenstein 2013).

Given that ranchers produce and sell the fibre individually, the volume produced is too small, leaving them with no other option but to sell the fibre to intermediaries for relatively low prices. Producers are unable to access international buyers, which consist of a very small number of Italian companies that have a long working relationship with the traders. According to interviews, international buyers require large volumes of fibre (between 1000 and 5000 Kg), a sustained level of quality over time, and a continuous supply. No individual fibre producer can fulfil these requirements on his own, and neither can a small group of producers. The guanaco fibre market is thus characterized by significant buyer power relative to negotiating capabilities, which limits the ability of the latter to capture more than a small portion of the value generated throughout the guanaco value chain (Guirola et al. 2009).

Although guanaco fibre has been exported in large quantities and for a long time to Europe, it is not as highly valued as vicuña fibre, which is considered "a status symbol" (Lichtenstein 2013). According to fibre experts, these two fibres have similar physical attributes, colour, and thickness, making them very difficult to distinguish even with a microscope (Proceedings of GEF Workshop, 2012). The potential for fibre mixing (Kasterine and Lichtenstein 2018) and the fact that the price of guanaco fibre is lower than vicuna fibre (Marino pers. comm., 2018) has led to some misuse in the industry (Kuffner pers. comm., 2015). The potential for mixing has also been observed in the cashmere sector, where yak and fine Merino sheep fibres have similar properties to cashmere (Cashmere and Camel Hair Manufacturers Institute, 2014).

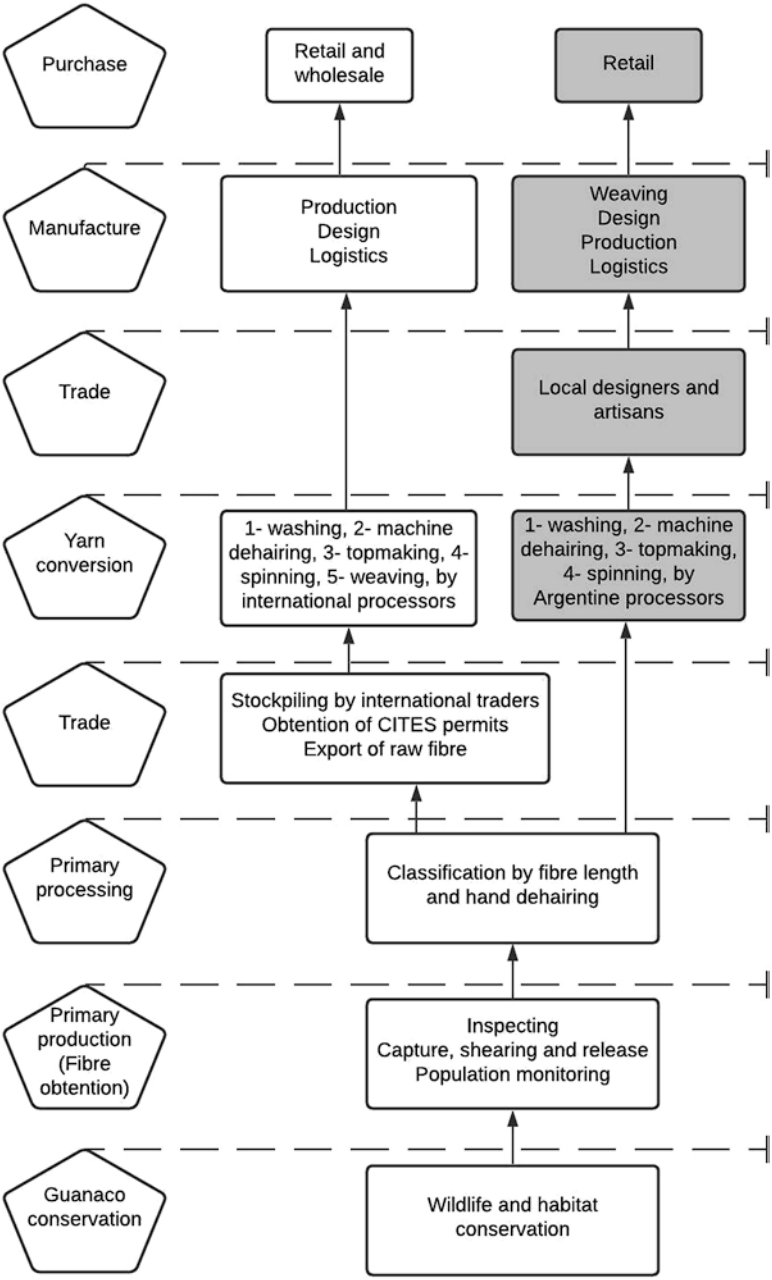

Fig. 7.4 Guanaco production and processing stages. After primary processing, fibre is either exported with limited added value (left branch); or processed in Argentina (in grey)

7.5.2 Fibre Commercialization

The fashion industry is undergoing a paradigm shift in which it is promoting the choice of higher quality natural raw materials, production with care for the environment, good management practices and animal rights, in smaller quantities and the generation of quality employment, not only in the initial part of the chain or in the design of the product, but in each of the links that make it up. In this context, the fibre obtained from wild guanacos managed with high animal welfare standards and following good practice protocols could be framed within this new way of consumption, which would help to revalue guanaco fibre as an environmentally sustainable fibre that is beneficial for the communities.

The guanaco fibre business operates in a highly complex and competitive market, due to the relatively small volume of production in the textile world and the fact that luxury fibres, in general, are becoming commoditized, so there is a strong need for guanaco fibre producers to differentiate themselves. The increasing volumes of cashmere fibre with high-quality standards make it very difficult to compete directly with these producers. In this regard, several global companies offer cashmere fibres and blends from as low as US$80/Kg. There are also cashmere yarns with 15- or 16-micron fibres that sell for around US$100–120 FOB/Kg. One way to differentiate guanaco producers themselves is by obtaining international animal welfare and traceability certificates that allow them to add value to their products. Recently, Wildlife Friendly Enterprise Network (WFEN) began certifying wild guanaco fibre obtained through sustainable practices to improve the positioning of certified products in the national and international markets. Some buyers are interested in Wildlife Friendly certified guanaco fibre and have offered U$S 200 per kilo of raw fibre (Novaro, pers. comm.), which represents one of the highest values proposed for guanaco fibre. However, the commercialization of guanaco fibre still faces challenges. The first issue is the lack of an established transparent market for the fibre and a small overall market demand for guanaco processed goods. The similarity between guanaco and vicuña fibre poses the need to develop easy methods to help authorities that control exports and imports to differentiate them and ensure that guanaco is commercialized as such (Lichtenstein and Carmanchahi 2012). In many cases, guanaco fibre producers face constraints in realizing the economic potential of their system due to high transaction costs, such as long distances to markets, processing plants or final consumers; lack of formal markets; poor access to information; lack of fair contracts; difficulties in marketing and creating distribution channels; limited access to credit facilities; lack of adequate communication systems; and excessive government bureaucracy.

7.5.3 Bottlenecks for the Fibre Commercialization

The guanaco fibre market has certain characteristics that influence its dynamics. The existence of strong competition with substitute products such as synthetic fibres, protein fibres, and even wool means that buyers have a high propensity for these products and generate greater bargaining power. In addition, these buyers have access to the network of international companies that process fibre and manufacture luxury clothing. As such, they have access to market price information, creating a strong asymmetry with producers. Although the market for guanaco fibre remains attractive because of its relatively small size and the quality of the product, barriers such as land ownership or access to land with abundant guanaco populations, complicated live shearing regulations, availability of trained personnel to carry out the activity, variable annual production volumes (for shearing in the wild) and heterogeneity in quality of the fibre offered to the market make it less attractive for new producers to enter the market. While shearing guanacos in captivity clearly indicates that it is not a viable activity due to the cost structure, shearing wild guanacos is viable and therefore recommended as a business model (Guirola et al. 2009).

The lack of differentiation of guanaco fibre and adequate market positioning, coupled with the inability of producers to capture value due to their weak price negotiating position, has led to price erosion and undermined producers' profitability. To reverse this situation, producers need to engage in initiatives that expand the market for guanaco fibre products through a strategic and integrated marketing approach concerning other actors in the value chain, forming some kind of partnership. This type of association, which fosters cooperation between producers, would increase their market power by reducing costs through the exchange of equipment and know-how and, at the same time, negotiate better sales prices due to the larger volumes of fibre available to them. On the other hand, the definition of clear policies in relation to the use of the species and the generation of certain tax benefits for producers could be a good incentive for those ranchers who want to start with the activity. Wild guanaco management activities could also generate additional income through alternative uses such as ecotourism.

7.5.4 Meat Production, Implications for Wild Populations

The harvest of wild guanacos to commercialize meat has recently been approved in the National Management Plan for the species (SAyDS 2019). The few experiences carried out so far have not reported costs and economic benefits associated with them. No information is even available on profitability aspects of meat production from the experimental trials carried out by state agencies together with the private sector in 2018.

One factor that harms guanaco meat production is sarcocystiosis caused by a parasite (*Sarcocystis aucheniae* and *Sarcocystis masoni*) that develops intramuscular macro- and microcysts respectively. The consumption of infected meat, raw or undercooked, causes gastroenteritis in humans with nausea, diarrhoea, colic, and chills, symptoms caused by the action of a toxic substance contained in the cysts (Decker Franco 2015. See Chap. 4).

In 1981, the guanaco population in Tierra del Fuego (Argentina) was approximately 75.5% positive for sarcocystiosis (Cunazza et al. 1995). Likewise, the Guanaco National Management Plan (SAyDS 2019) reports 69% of the animals slaughtered; neither report details the percentage of animals affected by microcysts. Other experiences carried out in Santa Cruz province reported that 61% of the animals hunted with firearms for the commercialization of meat presented macrocysts of sarcosporidia. The same report mentions that 77% of the guanacos slaughtered for meat production using capture traps had sarcocystiosis (Final Report. Proyecto Estratégico Uso Integral y Sustentable del Guanaco Silvestre. 2019). The presence of macrocysts between muscle fibres is one of the main factors in the decommissioning of guanaco meat. Studies in Chile showed that microcysts were detected in 100% of the slaughtered animals (Skewes et al. 1999). Recently, 89.2% of the guanacos hunted during 2016 in Tierra del Fuego (Chile) had macroscopic findings of sarcoscystiosis and around 9000 Kg of meat had to be confiscated (Swanhouse 2016). In the 2019 harvest season in Tierra del Fuego (Chile), the main cause of seizures was the massive presence of sarcocystiosis, which forced the recall of 97 whole guanacos plus partial recalls of affected animals, totalling 6198 Kg seized (Soto Volkart and Molina Uriarte 2020).

The Chilean model of guanaco population management is based mainly on the meat harvesting from the wild populations present in the most southern distribution area in that country. Meat harvesting is mainly carried out by two companies working in Tierra del Fuego island, so the spillover of this productive activity from a wildlife resource, which is *res nulius* according to its National Constitution, is very low. From 2004 to 2016, these companies harvested a total of 22,716 guanacos, which represented 87% of the quotas granted. The average boneless meat obtained per animal was 23 Kg. The price of meat has fluctuated between 1999 and 2016 with an average of U$S 4.75/Kg (Soto Volkart and Molina Uriarte 2016), the 2016 value being U$S 6.26/Kg. A cost analysis recently conducted by one of the companies that carries out this activity mentions that the cost of obtaining 1 Kg of guanaco meat is U$S6.92 (Swanhouse 2016), therefore, this company is currently ceasing this activity. This situation is aggravated by the fact that 89.2% of the meat obtained contained sarcocystiosis. On the other hand, with potential use of 22,716 hides and approximately 4543 Kg of fibre from the shearing of hides (assuming one hide/guanaco slaughtered and 200 grams of fibre/hide sheared), only 5.6% of the hides and 0.44% of the fibre have been sold (Soto Volkart and Molina Uriarte 2016). The low placement of these products is surprising considering the high volume available. This may be due to the fact that the market for this type of fibre is very particular as it seeks a high-quality product obtained under sustainable conditions and considering animal welfare. This market is associated with certifications of origin and sustainability, not only biological but also taking into account the social spillover of the use of a native wild species. Nor has any interest been detected in Chile for the industrial development of products made from guanaco hides, because they are difficult to tan due to their irregular thickness and have superficial veins that deteriorate the quality of the final product (Verscheure 1979; Verscheure et al. 1980). However, more recent analyses on the quality of leather in Argentina show that it has acceptable physical characteristics for use in footwear manufacturing (Martegani 2017).

In Argentina, the incidence of sarcocystiosis is coupled with inexperience in the method of slaughtering the animals. In an experience of hunting in 2016, of 20 guanacos slaughtered for meat utilization in a farm in Santa Cruz province, 65% of the meat produced had to be confiscated due to bullet impacts that caused contamination by burst bones, contamination due to waiting between hunting and slaughter, incorrect bleeding, in addition to the presence of sarcocystiosis (Report by the Director of Food Products, Provincial Agrarian Council, 28 October 2016). The presence of sarcocystiosis in guanaco meat is an issue that still requires studies to establish which age categories, sex, and geographical areas have a lower incidence of the parasitosis, so that the best areas to carry out this activity can be adjusted and thus reduce the loss of product. Meanwhile, evidence suggests that wild guanacos harvesting for their meat does not bring economic benefits to producers or to the conservation of this species.

A sub-product of animal harvesting for meat is the production of fibre from slaughtered guanacos. The supply of fibre from dead animals on the market poses a risk for enterprises that shear live animals because the same product is obtained at a much lower cost. In addition, it puts at risk the positioning of the fibre, both nationally and internationally, since, as mentioned above, the public seeking this fibre belongs to a select niche market that values the history of obtaining it. The bad image that can be caused by a campaign such as those carried out by animal rights organizations can impact negatively on the commercialization of all-natural fibres in Argentina. According to the words of Claire Bergkamp, head of sustainability and ethical trade at Stella McCartney company: “It is not that luxury companies will be rewarded for embracing sustainability, but they will be punished if they don’t” (https://www.linkedin.com/in/claire-bergkamp-2a6ab65/) and clearly, dead animal fibre is not a desirable raw material for these companies. In addition, sheep wool production could also be affected by these initiatives because, if these actors identify that guanacos are slaughtered for their fibre, there is a risk of a boycott of receptive markets for sheep wool from Patagonia.

7.6 Adaptive Management of the Wild Species

To conclude this chapter, we analyse whether the actions taken since the approval of the National Management Plan in 2006 have met the criteria for adaptive management. To this point, we first briefly outline the general guidelines of adaptive management, in order to contextualize the experiences related to guanaco management in Argentina.

Socio-ecological systems pose complex scenarios, based on a large number of variables that comprise them (e.g. biological, political, demographic, social) and the unpredictability in which these factors can interact with each other. Adaptive management (Holling 1978) has been proposed as a systematic approach to deal with these complex systems for deciding how to act in the face of risk and uncertainty and improving resources management and conservation (Salafsky and Margoluis

2003). Adaptive management emphasizes learning through management (Walters 1986) and it has a specific structure in the decision-making process (Allen et al. 2011). Salafsky and Margoluis (2003) also define adaptive management as the type of approach that incorporates research into action, involving iterative processes that serves to reduce uncertainty, build empirical knowledge and improve management over time in a goal-oriented and structured process (Allen et al. 2011). Altogether, all the steps involved in adaptive management can be integrated into an iterative cycle of decision making, monitoring, and assessment, such as the one presented in Fig. 7.5.

7.6.1 *Adaptive Management in Guanacos*

The first step in adaptive management is to clearly define the problem facing the natural resource to be managed or conserved. The management of guanacos offers a great challenge, given the profound complexity of the socio-environmental systems in which the species is distributed. In Argentina, a multiplicity of stakeholders are connected and interrelated, with dissimilar interests, motivations, and historical and cultural characteristics that are not always easy to align. In this sense, the main problem detected is the high degree of conflict that the livestock sector has had with the guanaco due to an alleged competition for forage resources (see Chap. 3). This conflict has led to heavy hunting pressure, both legal and illegal, which, together with the severe degradation of the environment due to overgrazing caused by livestock unsustainable management, resulted in a drastic decline in guanaco populations in Patagonia (Fig. 7.6). Consequently, CITES suspended exports of guanaco products from Argentina until a National Management Plan for the species was developed (see Chap. 6).

Following this prohibition, a deliberative and participatory process began in Argentina that concluded with the design and elaboration of the Guanaco National Management Plan in 2006 (see Chap. 6). The main operational goal of the plan was to coordinate actions, programs, and initiatives for the protection and use of the species to ensure the conservation of its biological, economic, and cultural roles through its sustainable use. A basic concept in the formulation of the whole plan was related to the generation of a productive alternative that, in addition to generating an economic income, would allow a change in the negative perception that livestock producers had of the guanaco. This plan established the first management norms and protocols based on scientific research and generated a framework for the protection of the species. The implementation of the GNMP was reflected in the adhesion of several provinces and the implementation of management activities, although these were not sustained over time. The regional context during this period was complex. At the same time, a process was taking place that led to a sharp reduction in the sheep population in most of Patagonia. This process was encouraged by external factors, such as the fall in the market value of sheep wool, and by internal factors, such as severe soil degradation (desertification). Those fields with better primary

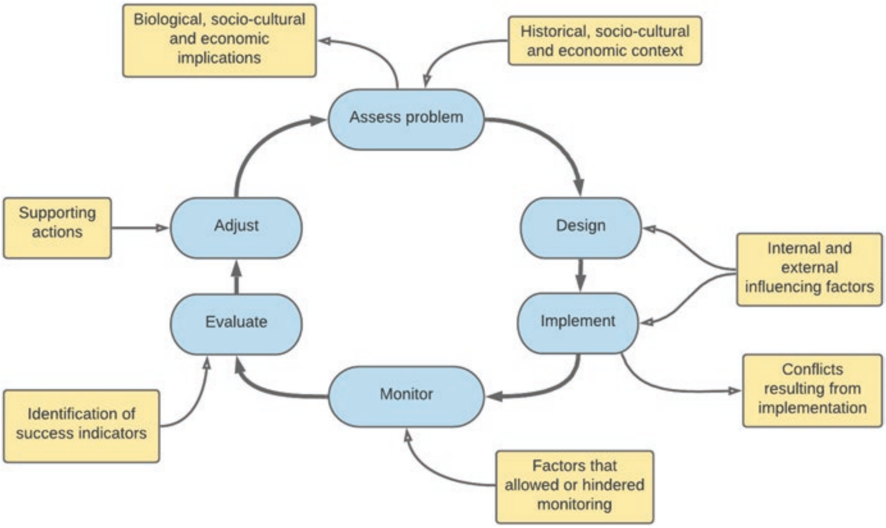

Fig. 7.5 Schematic representation of the steps in the adaptive-management cycle. The light-blue shapes show requisite steps in the selection of management actions that are to be carried out in an adaptive framework. The yellow boxes represent the context in which the detected problem requires intervention, the factors that can influence the adaptive management steps, and the possible consequences or implications that each of these steps could have

productivity were reconverted to cattle production. However, in many other cases, fields were abandoned, leaving large areas free of anthropic pressure for guanaco populations and also for predators, which began to recover territory and increase their abundance. The increase in the abundance of guanacos in some areas of the Patagonian region, together with an increase in the density of predators, further complicated sheep production and aggravated the conflict with the livestock sector. While it is true that in some areas of the Patagonian region, such as the south of the Atlantic coast of Santa Cruz province, this increase was significant, in others it was not, and the application authorities based their decisions on the perception of the livestock sector, which generalized and overstated this increase without a scientifically based population survey of the entire Patagonian region. In this regard, during 2014 and 2015 the National Ministry of Agriculture, Livestock and Fisheries carried out a population survey (Bay Gavuzzo et al. 2015) at a regional scale. This study was highly criticized by scientific and technical sectors due to serious deficiencies in the design of the survey, as well as the very high levels of error detected, which limited the usefulness of the estimates provided by the report to assess guanaco abundance. For this reason, and because the spatial scale did not allow it, these estimates could not be considered and validated as a technical tool to contribute to the management of the species (Rey et al. 2016).

Although the GNMP originally addressed important aspects related to the generation of information necessary for the management of the resource, such as the promotion of sustainable practices for the species, the generation of regulations to

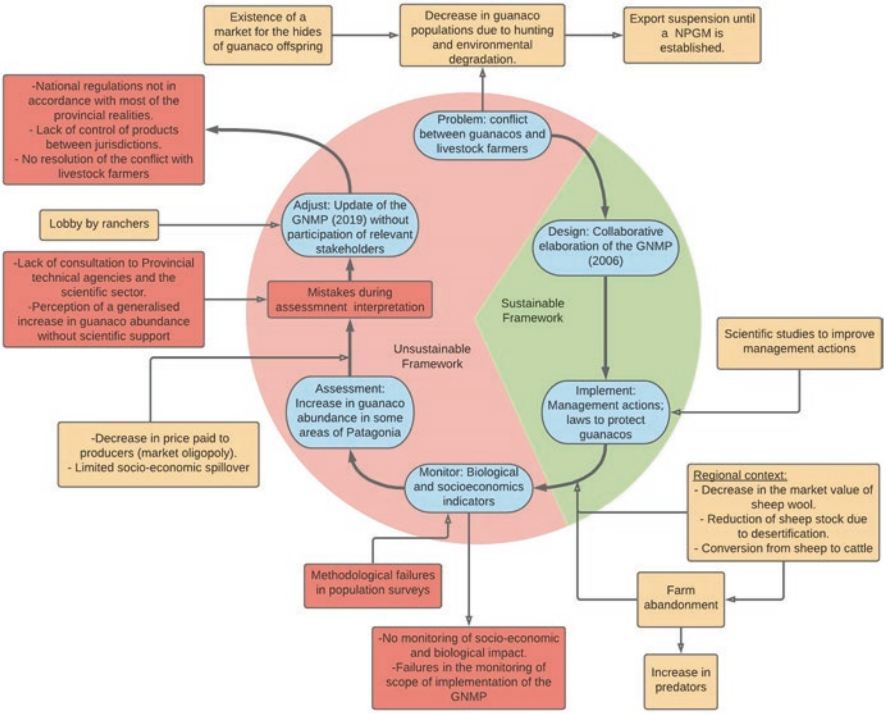

Fig. 7.6 Flow chart synthetically outlining the recent history of guanaco management in Argentina. Light-blue shapes show the steps that represent adaptive management, based on the scheme in Fig. 6.4; salmon-pink shapes represent the external influences and specific contexts that influenced each stage. Red shapes indicate errors or conflicts that arose during the process. The underlying concept in guanaco management is that of sustainability (indicated by the green section of the circle, providing a framework for each of the steps). It is important to note that the diagrams representing adaptive management describe a cycle (Fig. 7.5) but in the case of guanaco management, we consider that this cycle is not closed, since, when some errors were generated in the monitoring and evaluation process, incomplete adjustments were established that originated new conflicts and, therefore, did not solve the original problem. This break is represented by the light-red section of the circle, which indicates the lack of a resulting sustainability framework

guarantee the conservation and use of the guanaco and the strengthening of the structure for the control of activities, it did not mention concrete monitoring actions to self-evaluate its functioning, nor did it stipulate periods for updating the Plan. The GNMP did mention the need to assess the sustainability of the use of the species using ecological, economic, and socio-cultural indicators, but it delegated this responsibility to regional management programs, without specifying specific actions.

Other important aspects, such as the scope of the implementation of the plan at a national level and the monitoring of economic and social variables, were not adequately followed up. One of the key factors influencing management decision-making is the commercialization of products obtained from the use of guanacos and also the socio-economic spillover of the activity. The lack of a transparent and continuous market for guanaco products, as well as the lack of support from the State in the form of incentives and tax benefits, negatively influenced the interest of producers in incorporating guanaco management as a complementary activity. This generated little socio-economic spillover from this activity.

Fifteen years after the first GNMP was approved, several factors converged to promote the modification and approval of a new GNMP in 2019. Among them, a change in national public management towards more neoliberal policies that favoured the commercialization of the resource, and strong pressure from some producers in Southern Patagonia to different provincial and national state sectors, based on the need to control the "excessive increase in guanaco populations'‘. This Plan was based on inaccurate, incomplete and biased information because it was generated without input from the technical areas of most of the provinces, or groups of specialists in guanaco management and conservation. Therefore, a generalized increase in the population throughout their distribution range was erroneously considered, and activities were authorized that should have been established for limited areas where there was a real population increase. Thus, the commercialization of meat and fibre (including that of slaughtered animals) was allowed, without taking into account the conservation status of the populations throughout their range or the sustainability of management actions (see the introduction chapter for the conservation status of the populations and Chap. 6 for more information on related public policies). This new plan brought new conflicts, associated, for example, with the control and transit of products, since in many cases provincial regulations had been decoupled from these new national regulations, and products that were permitted only in some provinces began to circulate in different jurisdictions.

In conclusion, although the management of the species embraced the adaptive management system in its origins, accumulated failures in implementation, monitoring, and evaluation, coupled with sectoral pressures, meant that a virtuous circle could not be completed and today, the problem initially enunciated has not only not been solved, but has become more complex.

In order to advance in the resolution of the conflict between the livestock sector and the guanaco, it is necessary to implement actions based on the concept of coexistence, which proposes the incorporation of management measures to facilitate the compatibility of the traditional production system with wildlife, avoiding the alteration of the life history of native species. This paradigm promotes not only coexistence between native and domestic herbivores, but also the use of non-lethal tools to control predation (Novaro et al. 2017). The implementation of initiatives that favour coexistence requires integrative solutions that combine livestock production and species conservation on the same land. To this end, it is necessary to adapt herbivore loads and grazing regimes to reconcile both objectives.

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Chapter 8
Historical Perspective and Current Understanding of the Ecology, Conservation, and Management of the Guanaco in the Chilean Patagonia

Benito A. González, Pablo Acebes, Paulo Corti, Moisés Grimberg, Esperanza Iranzo, Juan E. Malo, Claudio A. Moraga, Ronald J. Sarno, Oscar Skewes, Nicolás Soto, Juan Traba, Solange Vargas, and William L. Franklin

8.1 Introduction

Chile contains an ecologically diverse fraction of the great Patagonia territory that dominates the extreme southern cone of South America (Fig. 8.1). The Chilean Patagonian steppe and scrublands cover around 30,000 km^2 (Olson et al. 2001) of the continental Aysen (~30%) and Magallanes districts (~40%), plus the northern portion of Isla Grande of Tierra del Fuego (~30%). The Chilean Patagonia in Magallanes also includes subpolar forest (~123,000 km^2) and around 3000 islands

B. A. González (✉)
Laboratorio de Ecología de Vida Silvestre, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile

IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile
e-mail: bengonza@uchile.cl

P. Acebes
IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile

Terrestrial Ecology Group. Ecology Department/Centro de Investigación en Biodiversidad y Cambio Global, Universidad Autónoma de Madrid, Madrid, Spain
e-mail: pablo.acebes@uam.es

P. Corti · E. Iranzo
Laboratorio de Manejo y Conservación de Vida Silvestre, Instituto de Ciencia Animal, Facultad de Ciencias Veterinarias, Universidad Austral de Chile, Valdivia, Chile
e-mail: pcorti@uach.cl; esperanza.iranzo@gmail.com

M. Grimberg
IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile

Gerencia de Áreas Silvestres Protegidas, Corporación Nacional Forestal, Santiago, Chile
e-mail: moises.grimberg@conaf.cl

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_8

in the archipelago of Tierra del Fuego, including Navarino Island in the south. Throughout this entire region, bordered by Argentina to the east, the open landscape is a continuum without obvious terrestrial barriers, facilitating the free movement of fauna. Only Tierra del Fuego is isolated from the continent by the Strait of Magellan, which has resulted in a unique and relatively depauperate biogeographic faunal patterns with the guanaco standing out as the only large mammal on the island (Osgood 1943; Texera 1973). The proximity of Chilean Patagonia to the Pacific Ocean and Andean Mountain range generates a climate that gradually ranges from rainy-cold and humid in the west to a dry-cool and arid climate toward the east (Pisano 1977).

It is this region, characterized by mountainous landscapes, valleys, extensive plains, regional forests, and the vast plateau of steppe shrubs, grasses, and herbaceous vegetation (Pisano 1974) where the guanaco is especially abundant in Chile. The environments utilized by the guanaco have a seasonal productivity greater than that observed in arid environments of Argentine Patagonia near the Atlantic Ocean. This greater abundance of forage supports large populations of guanacos, which

J. E. Malo · J. Traba
Terrestrial Ecology Group. Ecology Department/Centro de Investigación en Biodiversidad y Cambio Global, Universidad Autónoma de Madrid, Madrid, Spain
e-mail: je.malo@uam.es; juan.traba@uam.es

C. A. Moraga
Centro de Estudios del Cuaternario de Fuego-Patagonia y Antártica, Fundación CEQUA, Punta Arenas, Chile
e-mail: clmoraga@gmail.com

R. J. Sarno
Department of Biology, Hofstra University, Hempstead, NY, USA
e-mail: Ronald.sarno@hofstra.edu

O. Skewes
Departamento de Ciencia Animal, Universidad de Concepción, Concepción, Chile
e-mail: oskewes@udec.cl

N. Soto
IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile

División Protección de Recursos Naturales Renovables, Servicio Agrícola y Ganadero, Punta Arenas, Chile
e-mail: nicolas.soto@sag.gob.cl

S. Vargas
IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile

Departamento de Biología, Universidad de La Serena – Universidad Católica del Norte, Antofagasta, Chile
e-mail: svargas@userena.cl

W. L. Franklin
IUCN SSC South American Camelid Specialist Group (GECS), Santiago, Chile

Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA, USA
e-mail: wlf@myomnitel.com

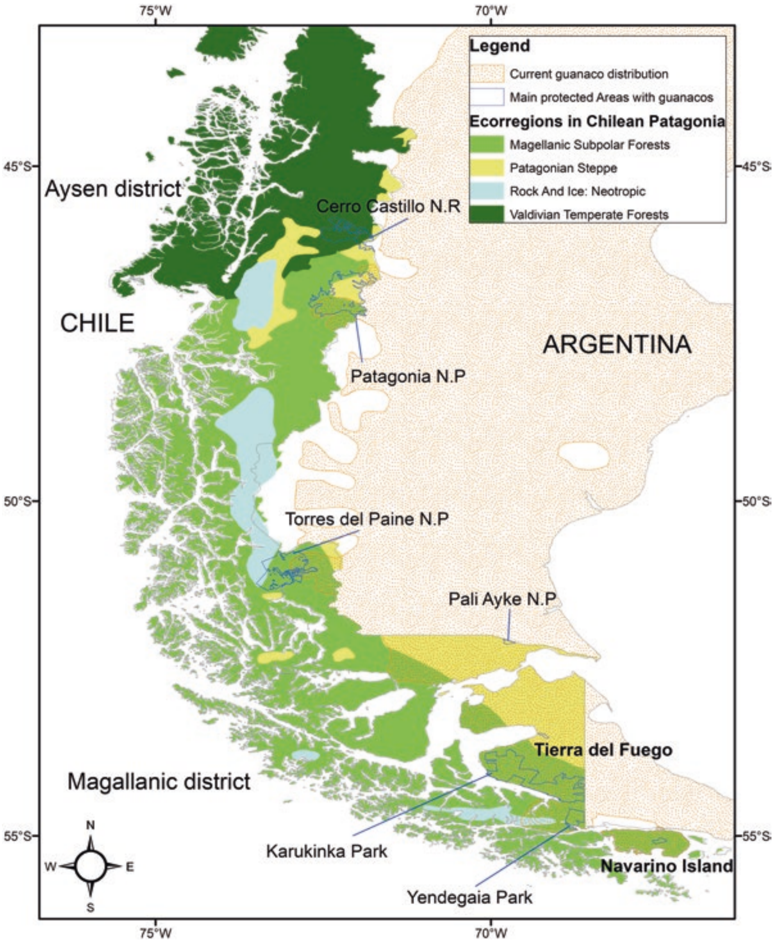

Fig. 8.1 Map of the Chilean Patagonia indicating the locations of the main ecoregions (Olson et al. 2001) and guanaco populations in the Aysen and Magallanes districts, and Argentinean Patagonia. (Based on WCS 2014)

like other populations in Patagonia were drastically reduced over the past century until the 1960s when national parks and protected areas were established (Cunazza 1992). Thereafter, guanaco populations slowly recovered and expanded, leading to a scenario of increasing conflicts in recent decades with the forestry and livestock industries in the region.

Details of the biology and ecology of guanaco populations in Chile have been studied extensively in the last two decades, resulting in around 35% of all the publications on the species. These works were a continuation of a tradition of Chilean and international scientists detailing characteristics of the species that included Abbe Juan Ignacio Molina (1782, 1788, 1808) at the end of the eighteenth century, followed later by Father Rafael Housse (1930) and Wilfred Osgood (1943) of the

Field Museum of Natural History of Chicago, USA. In the Magallanes district of Southern Chile, the pioneering works of Kenneth Raedeke (1978) and William L. Franklin (1982, 1983, 2011) and his research team in Tierra del Fuego and Torres del Paine National Park made significant contributions to our knowledge of the guanaco not only in Chile, but also throughout its distribution.

At present, there are several working groups from Chilean institutions conducting studies in the Chilean Patagonia that are contributing to our basic knowledge and management of the species. Their aim has been to maintain viable guanaco populations in protected parks and to seek strategies that promote the coexistence of guanaco conservation programs, livestock, and forestry interests. The overall goal in this chapter is to highlight the research that has been carried out in Chilean Patagonia over the past half century and to describe the main advances in guanaco ecology, conservation, and management. Topics to be addressed include: (1) characterization of guanaco research history; (2) a summary of information on the abundance and growth of Patagonia guanaco populations on Isla Grande de Tierra del Fuego and continental Chile; (3) a highlight of advances in our knowledge of guanaco ecology; (4) regional conservation strategies, including sustained productive management; (5) our understanding of the interactions of guanaco and livestock across spacial and trophic levels; (6) perceptions of conflict; and (7) perspectives of future research and management needs for the guanaco in the Chilean Patagonia.

8.2 History of Guanaco Research

The history of guanaco research in the Chilean Patagonia is characterized by three non-exclusive chronological periods that generated a body of knowledge that reflect Chilean changes in guanaco conservation and management objectives over the past half century. The first period was led by foreign investigators that worked in the 1970s in Tierra del Fuego and later moved their focus to the Torres del Paine National Park in the 1980s. These efforts documented fundamental biological information while concurrently supporting conservation efforts. The 1990s was characterized by experimental work that focused on guanaco management, as well as the prospect of commercial use of guanacos given the sustained growth of populations in far southern Chile. Most recently, from 2000 onwards, research has increasingly dealt with the growing conflict between sheep ranching and silviculture as the growing populations of guanacos, especially in areas of minimal protection, became increasingly a conservation focal point.

8.2.1 The First Decades of International Support: 1970s–1980s

The negative effects of Spanish colonization on the Chilean fauna, combined with persistent illegal hunting of the guanaco and the lack of knowledge of basic aspects of the biology of the species, stimulated the Forestry Division of the Agricultural and Livestock Service of the Ministry of Agriculture of Chile to establish a Cooperation Agreement with the United States Peace Corps in 1969. The goal was to initiate a program of study through the University of Washington to assess approaches to enhance the recovery of wildlife species that were deemed to be the most endangered in Chile, among them the guanaco. A PhD student, Kenneth Raedeke, conducted the first modern, in-depth, field study on the species after arriving in South-Central Tierra del Fuego, specifically to the property of the *Sociedad Agrícola de Reforma Agraria* (S.A.R.A.) Cámeron from 1972 to 1975. His research provided important insights and set the stage for subsequent work by sparking interest in the species from the Chilean and international scientists that followed. His research had a strong quantitative component that emphasized population dynamics, including patterns of distribution, movement, body growth and condition, reproduction, mortality, natality, food habits, aging techniques, population structure, social organization, food habits, and competition with sheep. Many of his contributions were published in 1979 in Technical Document No. 4, "El Guanaco de Magallanes, Chile. Its distribution and biology", edited by CONAF. Dr. Raedeke (1982) hypothesized that the absence of guanacos in the prairies of Tierra del Fuego during the 1970s had been caused by their displacement by livestock activities, forcing guanacos into marginal habitat of *Nothofagus* forests. In 1974 the project "Conservation and Management of Guanaco on Tierra del Fuego Island" was established with the efforts of CONAF under the direction of Mr. Claudio Cunazza (1974–1985), Mr. Juan Ivanovic S (1985–1988), Nicolás Soto V (1988–1997), and Alejandra Silva (1998–1999). Since 2000 this project has been continuously directed by the Division for the Protection of Renewable Natural Resources of the Agricultural and Livestock Service of the Magallanes district.

Broad research efforts were continued on the guanaco through the field studies of William L. Franklin from Iowa State University from 1976 to 2000. His first several years of year-round field research were centered in Central Tierra del Fuego, but were then shifted to Torres del Paine National Park on the mainland. In collaboration with the Chilean National Forestry Corporation, Franklin's research at Paine became known as "Proyecto Puma" to reflect the long-term monitoring and study of the predator/prey dynamics. Proyecto Puma involved the efforts and collaboration of many individuals, organizations, and government agencies. The project produced an array of information about the mammalian fauna and plant communities of the northern Chilean Patagonia through master-of-science and doctoral students who collected field data year-around. Dr. William Franklin's main contribution to guanaco research, among other topics, was to develop studies focused on the behavioral ecology, following a long history of this kind of research in South American

Table 8.1 Summary of basic research on guanacos from 1970s to the mid-1990s

Topic	Scientific reports and articles
Population dynamic of guanaco in South-Central Tierra del Fuego	Raedeke (1978, 1979)
Habitat use and diet of the guanaco	Raedeke (1980, 1982)
General approach to biology, ecology, and importance to human of the guanaco (and vicuña)	Franklin (1982, 1983)
Behavior of the guanaco	Wilson and Franklin (1985), Garay et al. (1995), and Ortega and Franklin (1995)
Live capture of guanacos	Jefferson and Franklin (1986), Franklin and Johnson (1994), and Sarno et al. (1996)
Habitat preferences	Ortega and Franklin (1988)
Biogeography in the Chilean Patagonia	Johnson et al. (1990)

Table 8.2 Principal guanaco studies conducted in Chilean Patagonia during the 1990s

Topic	Scientific reports and articles
Planning for guanaco sustainable management	Franklin and Fritz (1991), Bonacic (1993), Fritz and Franklin (1994); Cunazza and Oporto (1995), Oporto and Soto (1995), Franklin et al. (1997), Skewes et al. (1998a, b), and Torres (1995)
Evaluation of the population status and environmental descriptions	Cunazza (1992), Cunazza et al. (1995), Duran (1996), Soto (1998), and Bas and González (2000)
Analysis of potential products and markets	Soto (1994), Bas (1997, 2000), and González et al. (2000a, b)
Protection and recovery	Cunazza and Videla (1995) and Silva (1995)
Captive management	Bas et al. (1995) and González et al. (1998)
Legal and institutional framework	Soto (1998) and Iriarte (2000)
Molecular biological studies	Marabachvilli et al. (2000) and Sarno et al. (2000)
Interaction with forest and livestock production	Skewes et al. (1998c)

camelids beginning with Carl Koford, both of whom conducted vicuña research in Peru (Koford 1957; Franklin 1978, 1983). Two important articles written by Dr. Franklin that continue to be widely cited today compared the biology, ecology, and inter-relationship among humans and the South American camelids (including the guanaco and vicuña (Franklin 1982, 1983). During the mid-1990s additional research from Proyecto Puma included the sustainable use of S.A. camelids, behavioral ecology insights centered on newborns and patterns of juvenile survival and future fitness, and interaction between pumas and guanacos (see specific sections in this Chapter) (Table 8.1).

8.2.2 Population Management Research: 1990s–2000s

During the 1990s, research in Chile was focused on promoting and assessing efforts that documented and informed the protection and recovery of the guanaco in Southern Patagonia, including the early steps that were made to promote sustainable use (Table 8.2). During this period 27 reports and publications were published, including assessments of plans for sustainable management of guanacos, evaluation of the status of distinct populations and habitats, analysis of potential products and markets, legal and institutional frameworks for management and harvesting populations, molecular biological tools and related insights, and the dynamics of guanacos on silviculture (habitats) and on livestock production.

A series of publications by Franklin and Fritz (see Table 8.2) emphasizing the importance of sustained guanaco utilization brought international attention to the challenge of conserving and managing guanacos in southern Chile. The successful recovery of large populations of guanacos on Tierra del Fuego was producing a growing complaint from the traditional sheep-ranching industry under the premise that guanacos were having a negative impact on their profits. The theme of "use it or lose it" was advanced, suggesting that appropriate guanaco conservation and management needed to include a demonstrated economic return that otherwise would result in the return of widespread poaching and population decline.

To formally assess the potential impacts of controlled harvest the project "Productive and Sustainable Management of the Guanaco in Southern Tierra del Fuego" was carried out from 1996 to 1999 as part of a long-term program that was or first promoted and sponsored by the Chilean National Forestry Corporation (CONAF). Implemented by CONAF and co-financed by the Magallanes' Government, the study was carried out by the research teams of Juan Carlos Durán (1996) from the University of Chile and Oscar Skewes (1997–1999) from the University of Concepción. The project, centered in 200,000 ha surrounding Russfin of Cameron ranch in central Tierra del Fuego, was a milestone in guanaco conservation in the Patagonia of Southern Chile because it initiated the commercial and sustainable use of the guanaco.

The important results of these projects included:

1. Development and evaluation of in-situ capture and hunting techniques. Techniques that incorporated the massive capture of live animals were ultimately not recommended because of low yields and high costs. Selective hunting was evaluated and ultimately recommended based on technical, economic, and animal welfare advantages when considering the implications of more precise targeting of individuals on the broader management of the population.
2. Studies of population dynamics and harvest models. The target research population was in a high growth phase ($r = 0.11$) with high birth- and low-death rates, which theoretically would support an estimated annual extraction quota of 1700 individuals by assuming a logistic-growth model ($K = 60{,}000$).
3. Study of guanaco interactions with ranching and forestry production. Primary productivity, specifically the wet meadows and steppe showed no deterioration

but were at their carrying capacity limit. However, more than two-thirds of beech-forest seedling regeneration were affected by guanaco browsing in the study area, compromising both quality and quantity of timber production.
4. Market study of guanaco products. The fiber obtained from shearing had high economic potential for development, because of its fineness as a natural product with favorable marketing value and environmental sustainability. Particularly, properties of meat (nutrition, taste, sight, smell, and moisture) offered high potential for national and international markets among game meats. Ultimately, the economic and social evaluation of guanaco-sustained utilization indicated that the harvest of 1700 animals annually was profitable utilizing meat and fiber, but not the capture of live animals by shearing and release.
5. Health studies related to sarcosporidiosis. Foxes and dogs were confirmed to be the definitive hosts for parasitic protozoan *Sarcocystis guanicoecanis*. Nevertheless, guanacos with macroscopic parasites were shown to be an intermediate host with an infection rate of ~63% in forested and ~18% in open habitats. Sarcosporidiosis seriously affects the commercialization of fresh meat, which can be treated with salt and dehydration for human consumption.

8.2.3 Present Times, the Study of Guanaco and Livestock Conflicts During the 2010s and 2020s

Several research branches have widened our knowledge of guanacos in Chilean Patagonia in recent times (see below section on Guanaco Ecology for a review on genetics and other recent studies), but following the conservation perspective of the historical account, here we focus in the contingent struggle between guanaco conservation and human activities in the Patagonia. Historical scenarios may help to understand the current context of conflicts involving guanaco conservation, sheep ranches, and management. The protection program of guanaco populations started in the 1970s with the goal of recovering populations to be used as a sustainable resource (see Sect. 8.2.2). The success of the program resulted in the expansion and population growth of guanacos in the forest mosaics and steppes in central southern Tierra del Fuego to the steppes of northern Tierra del Fuego, as well as in Chilean

Table 8.3 Main projects conducted after 2010 in Chilean Patagonia focused on guanaco and livestock interactions

Project topic	Institutions and years
Ecological interactions	Universidad Austral de Chile 2017–current; Universidad Autónoma de Madrid 2017
Socio-ecology, human dimensions of wildlife	University of Florida 2017–current; Universidad Austral de Chile 2015; Universidad Autónoma de Madrid – Universidad de Chile 2010–2011
Management	University of Florida 2017–current; Universidad Autónoma de Madrid – Universidad de Chile 2011

continental Patagonia (see section on population; Iranzo et al. 2017; Zubillaga et al. 2014a, b). This expansion included protected areas, private ranches, and forestry properties.

The recovery of habitats by guanaco populations during the last two decades (2000–2020) ignited a latent conflict with sheep livestock production with origins in the Patagonia colonization period. This has been the focus of national and international academics from different Universities (Table 8.3) during the past two decades. The research aims have included diagnosing, informing, and seeking strategies to resolve the conflict between guanaco and livestock production applying ecological and socioecological approaches.

Although this type of research is recent, the context of present conflicts started long before as noted by the Chilean historian Martinic (1957). Guanacos were reduced in abundance and distribution by the 1950s because of successful and profitable large-scale sheep ranching businesses with nearly 2 million sheep in southern Chile (Martinic 1992). This land occupation and the hunting of juvenile guanacos for pelt commerce until 1929 (see regulation section; Iriarte and Jaksić 1986) caused the species to be restricted in small populations located mostly in marginal habitats not intensively used for ranching (Martinic 1957). These marginal habitats were forests and forest-steppe mosaics mostly in southern Tierra del Fuego. Almost two decades later these accounts were confirmed by pioneer guanaco ecologists in the 1970s (Raedeke 1978; Franklin 1982; Franklin et al. 1997).

Two historical events are important to understand present conflicts from a social-ecological perspective. First, guanacos retreated from some areas and were drastically reduced in others for decades, leading to a new normality, i.e., ranches with an absence or extremely low numbers of guanacos were common. As a result, guanacos were restricted mostly to the protection of forest-steppe mosaics. Thus, the recovery of guanaco populations in recent decades has been a novel feature of the landscape for many ranchers. Secondly, after the 1950s several factors affected sheep densities, including the increased fragmentation and degradation of grasslands. Wool and meat commodities have always been linked to foreign-market price upheavals impacting sheep densities and ultimately Patagonia grasslands (Pisano 1985). In addition, land reform promoted subdivision and redistribution of former extensive ranches to smaller units purchased by new owners (Martinic 2006). This further negatively impacted grasslands as new ranchers adapted livestock densities and management regimes to lower costs and to make productions more profitable, mostly by overgrazing (Pisano 1985; Covacevich 2006). Although local changes in Chilean Patagonia were not as dramatic as the collapse and abandonment of some ranches in the Patagonian Provinces of Argentina (Chap. 3, Aagesen 2000), the cumulative grasslands degradation is recognized at present as a critical factor of livestock production throughout the district (Martinic 2006; Covacevich 2006). This realization has focused the attention on the land's capacity to support large herbivores (sheep, cattle, and guanacos), especially by wildlife managers, conservation ecologists, and ranchers (Hernández et al. 2017; Soto et al. 2018; Iranzo et al. 2017; Moraga et al. 2015; Oliva et al. 2019; Marino et al. 2020).

Since the carrying capacity of the Patagonia grasslands is directly related to the number of herbivores, it is an important consideration for sustainable management. With the recovery of guanaco populations in southern Chile, the initial goal of its conservation program was accomplished. In the early 2000s, the Chilean government issued leases for the sustainable harvest of guanacos (Soto et al. 2018). At first, the limited harvest was carried on in areas where there were both adequate guanaco numbers and conflict with the forest logging industry (Skewes et al. 1998c), but with time it opened up to other areas where sustainable harvest was possible. Interestingly, the harvest as a top-down process opened the opportunity to tackle the conflict between sheep production and guanaco conservation. But given the dependency on a private contractor requesting a particular harvesting quota, the process can be inconsistent because as a business it is subject to harvest logistics, weather, costs, and its dependency upon fluctuating international market demand and prices. In practice, this meant that the intent to harvest and reduce guanaco populations and conflicts with the ranching and logging industries could be at the same time limited and localized.

The social consequences of the guanaco recovery across the Magallanes region have been expressed both as a successful story of conservation and as an impact story of the guanaco overabundance to ranching and forest logging. In this context, perceived and documented impacts mix in local ranchers and logger's views, traditionally perceiving guanaco numbers as extremely high, consuming forage that was intended for sheep (Moraga et al. 2015; Hernández et al. 2017; Iranzo et al. 2017) and browsing extensively the lenga (*Nothofagus pumilio*) regeneration (Muñoz and Simonetti 2013; Martínez Pastur et al. 2016). Provided that ecological studies in Argentina indicate patterns of sheep competition are detrimental to guanaco (e.g., Baldi et al. 2001, 2004) and that it is possible to assume this also occur in Chilean Patagonia, neglecting the fact that the recovery of guanaco in Chilean Patagonia takes place in ranchers and loggers' properties may damage even more the current perceptions and backfire the conservation achievements. A coupled strategy of socially motivated ecological research in Chile has begun to address guanaco and sheep interactions considering current questioning and causes of conflicts, especially in ranches. Part of this research includes species distribution, forage consumption and behavior, and disease exchange. Additional research on the social aspects of conflict focuses on understanding the myriad of stakeholders' perspectives on the guanaco, its ecology, impacts, and management benefits to inform its management. This may open the door to additional types of management that include stakeholder participation (Moraga, unpublished). Certainly, one way to enrich top-down management includes participation of the different types of stakeholders at different stages of the management process (Pozo et al. 2021). For the moment, it seems that it is important to properly communicate the ecological and social evidence among stakeholders and promote the exchange between managers, scientists, and ranchers, involved in guanaco conservation and land management.

8.3 Guanaco Population Size

Currently, the guanaco population reached an estimated 270,000 and 300,000 animals in Chile, of which 95–97% are in the Aysén and Magallanes districts, within which 66–68% are in Chilean side of Tierra del Fuego (González and Acebes 2016).

Guanaco population in Magallanes has experienced a large increase since the mid-1970s when it was at its lowest. Hunting, and habitat degradation due to livestock overgrazing forced the last guanacos into private and public protected areas (Raedeke 1979; Baldi et al. 2016). Conservation programs were clearly successful in reversing trends, and the guanaco population experienced a significant recovery (Baldi et al. 2016). As a result of population increase and expansion, at present the main populations are located outside protected areas of Patagonia and Tierra del Fuego. Of these, two populations have been extensively monitored: Torres del Paine National Park (TPNP) and its surroundings, and the population that inhabits the south-central zone of Tierra del Fuego.

8.3.1 Population Abundance in Torres del Paine National Park and Surroundings

In the Torres del Paine (TPNP) area the species was severely threatened when the population fell to only a few hundred individuals in the mid-1970s (Franklin 1982). Since then, the population greatly increased, both in the protected area and the surroundings.

Two public administrations, National Forestry Corporation (Corporación Nacional Forestal, CONAF) and Agricultural and Livestock Service (Servicio Agrícola Ganadero, SAG) oversee collecting data on wild animals within the National Park and in the neighboring livestock areas respectively. As both administrations have carried out population surveys during the last number of years using basically the same transects and methodology (see Barría and Plana 2018 and Soto and Molina 2020, for details), observational data to evaluate temporal trends inside and outside the protected area can be used (Fig. 8.2).

Guanacos observed within TPNP have continuously increased since 1976, when just 572 individuals were seen in the post-reproductive season of 1975, then peaked in 2008 with 4471 animals. This was a 278% increase in 42 years with a basic average yearly increase of 6.5%. This trend has now apparently slowed down, with 1592 individuals censused in 2018. The best fit for these data was a highly significant and explicative quadratic regression (adjusted $R^2 = 0.71$; $F = 37.12$; $p < 0.0001$; Fig. 8.2a).

Guanacos observed in the livestock area of the Torres del Paine district, where the species was absent for decades, have also steeply increased in the last 20–25 years: 742 guanacos were observed in 1998 and 4193 in 2020 with maximum peak in 2019 of 4563 animals. This was a 465% increase in just 21 years, that equals

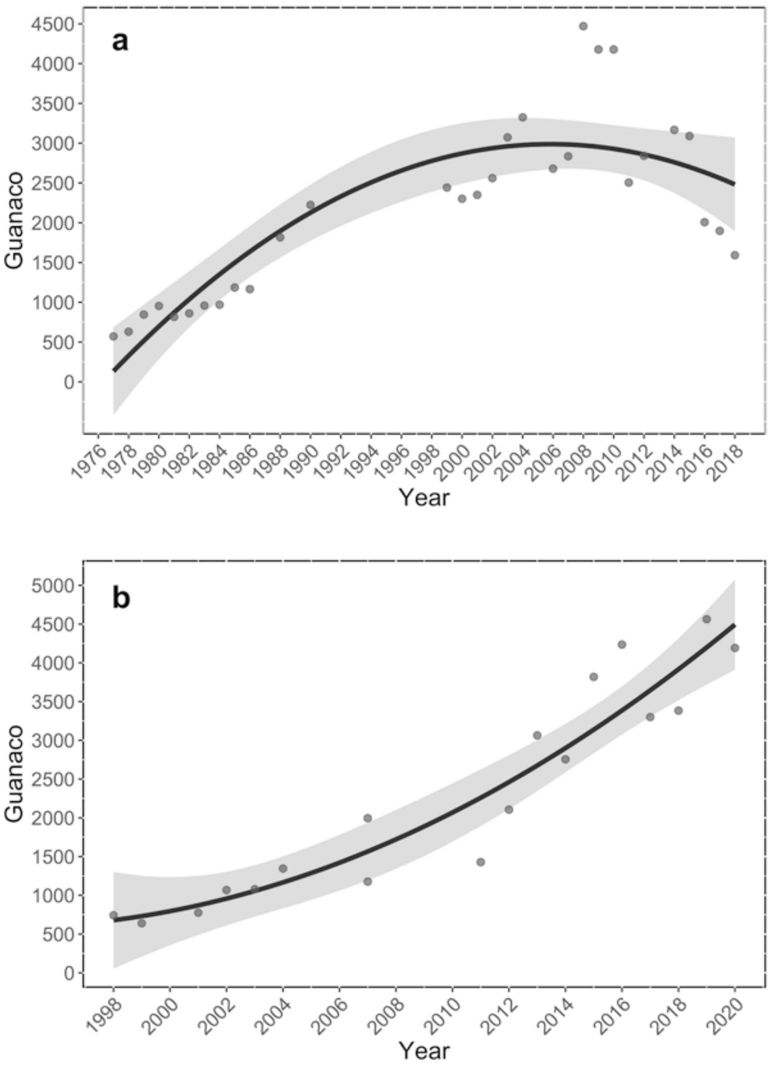

Fig. 8.2 Polynomial fit to number of guanacos observed in (**a**) Torres del Paine National Park (TPNP) between 1977 and 2018 during annual censuses carried out by the staff of Torres del Paine National Park Data provided by National Forestry Corporation (CONAF); and (**b**) outside TPNP between 1998 and 2019 during annual censuses carried out by the staff of Agricultural and Livestock Service (SAG). Linear trend is in blue, and 95% confidence interval in gray

a basic average of 22% yearly. In this case, the best fit is exponential, which suggests that the population size will be rapidly growing in the coming years (adjusted $R^2 = 0.88$; $F = 65.74$; $p < 0.0001$; Fig. 8.2b).

Information on the guanaco population size after Iranzo et al. (2018a) is available. While these authors estimated guanaco population size within TPNP and its surroundings (Torres del Paine district) at 13,000–17,000 individuals in summer and 13,000–22,000 in winter (Iranzo et al. 2017), Soto and Molina (2021) recently estimated around 8000 guanacos in Torres del Paine district and ca. 273,000 individuals in Magallanes. At present, the guanaco population in San Gregorio district is the second largest in Chile, only after Tierra del Fuego, with more than 96,000 guanacos.

Iranzo et al. (2018a) also provided estimates of population density, which varied between 10.2–25.6 individuals/km^2 in summer and 8.3–36.6 individuals/km^2 in winter. Soto & Molina (2021) offered similar figures, with between 6.5 individuals/km^2 in Porvenir district and 35.0 individuals/km^2 in the livestock area of Timaukel (Magallanes average: 13.0 individuals/km^2), Tierra del Fuego. All these data are among the highest ones described for the species (Schroeder et al. 2014), although they should be carefully considered as Distance software used in their estimation is extremely sensitive to aggregated distributions, as the guanaco has shown (Thomas et al. 2010). In any case, both observation and estimation data points to a steep increasing trend (near 500-fold increase in abundance) of guanaco population in the last 20–30 years.

As a conclusion, recent data suggest that the guanaco population is already well established in the surroundings of the Torres del Paine National Park, with a significant potential to grow and continue its expansion (Iranzo et al. 2018a). As guanaco abundance seems to decrease as distance to TPNP increases, a significant relationship between the protected area and the new areas recently colonized by guanaco appear to be reliably established (Iranzo et al. 2018a). This is a paradigmatic example of successful re-colonization by the guanaco, whose occurrence was extremely scarce 50 years ago.

8.3.2 Population Growth and Recovery in Chilean Tierra del Fuego

The history of the recovery of guanaco abundance in Tierra del Fuego Island (Chile) during relatively recent times is a wonderful example of successful conservation and recovery of a wild species. It should be remembered that this protective program started in 1974 when the country was politically struggling and by the state agency CONAF. The aim was the recuperation and incorporation of the species back into the productive matrix of the district. The program considered community education, poaching control, and biological studies of the species. It should be mentioned that this recovery program was applied entirely over an area of 2000 km^2 of private land and without impairing its productive function in Timaukel county of Tierra del Fuego. The first population estimate was in 1977 and repeated with the same methodology until the present. The method used to estimate the number of animals is King's (Robinette et al. 1974), which is a modification from Leopold (1933)'s method, counting guanacos from a vehicle by route. Dates and times are repeated year after year, with a record of the number, social composition, and the perpendicular observation distance. This same methodology is maintained to this day, although in recent times they have incorporated a Distance sampling model to expedite processing of the records. However, the estimates presented here include the original methodology for comparative purposes. The first count in 1977 estimated the population at 5372 animals in the Timaukel district on Tierra del Fuego Island in Chile. By 2020 the population was estimated at 77,405 animals (Table 8.4).

Table 8.4 Yearly abundance of guanacos in Chilean Tierra del Fuego over time indicated as total animals and percentage of estimated carrying capacity of the prospected area

Year	Population abundance	% of carrying capacity	Sarcoptes prevalence %[a]
1977	5372	9.0	
1978	5744	9.6	10.0
1979	6940	11.6	
1980	6693	11.2	
1981	8297	13.8	
1982	12,334	20.6	
1983	10,670	17.8	
1984	10,945	18.2	
1985	11,219	18.7	
1987	12,323	20.5	
1988	13,027	21.7	
1989	14,094	23.5	
1990	14,604	24.3	
1991	17,775	29.6	12.0
1992	20,774	34.6	
1993	16,410	27.4	
1994	17,626	29.4	
1995	21,445	35.7	
1997	20,777	34.6	
1998	28,978	48.3	
1999	27,809	46.3	
2000	28,935	48.2	
2001	38,841	64.7	
2002	38,363	63.9	33.7
2003	32,273	53.8	
2004	43,128	71.9	
2005	58,597	97.7	
2006	52,456	87.4	
2007	56,895	94.8	
2008	61,334	102.2	
2009	60,488	100.8	
2010	44,773	74.6	
2011	56,973	95.0	34.8
2012	45,325	75.5	45.7

(continued)

Table 8.4 (continued)

Year	Population abundance	% of carrying capacity	Sarcoptes prevalence %[a]
2013	51,635	86.1	36.0
2014	44,537	74.2	45.0
2015	34,431	57.4	21.0
2016	33,958	56.6	
2017	49,837	83.1	
2018	66,400	110.7	
2019	50,800	84.7	
2020	77,400	129.0	

Sarcoptes (mange) prevalence (%) is shown in some years as determined from hunted animals
[a]Calculated over total animals hunted

These same time-series data from guanaco population in Tierra del Fuego were analyzed by Zubillaga et al. (2018) who concluded that guanaco density was significantly correlated with female newborn and adult annual survival while annual precipitation correlated significantly with the fertility (females born per female per year), in contrast to population regulation mechanisms commonly seen in other ungulate species. The average carrying capacity of the guanaco population in Timaukel area (Cameron ranch) based upon the last 17 years was calculated at 46,694 guanacos (±9384 S.D.) (Zubillaga et al. 2018). Accordingly, the maximum carrying capacity should be ca. 60,000 guanacos. The population size has oscillated around this figure in the last 20 years with losses and recovery of size even well above this amount (Table 8.4). Zubillaga et al. (2014a, b) applied a regression analysis with finite population growth rate as the dependent variable, and as the independent variables total guanaco population size, sheep population, annual mean precipitation, and winter mean temperature (with and without time lags). The effect of population size was statistically significant, but the effects of sheep population size and the climatic variables on guanaco population growth rate were not statistically significant. The recovery of the abundance of the species in Chilean Tierra del Fuego is a great achievement. In addition, harvests have been made in the last years and in this way the species was incorporated into the local economy, while maintaining an abundant and recovered population.

An interesting and concerning aspect of the guanaco population of Tierra del Fuego is the prevalence of sarcoptic mange (*Sarcoptes scabei* var. *aucheniae*). In 2003, out of 355 animals analyzed (inspection of hunted animals) the clinical prevalence was 34%. In later years, the prevalence remained between 45 and 15% (Table 8.4). In guanacos from the continent, using the same methodology, the prevalence was 0%. The hypothesis that arises is to what extent has the puma in the continent (absent in Tierra del Fuego) contributed to lowering or mitigating the presence of the disease (Skewes and Aravena 2016, 2019).

8.4 Guanaco Ecology

Investigations on the ecological aspects of the guanaco in Chile are extensive, particularly in recent years. The works carried out in Chilean Patagonia have been diverse. Topics related to molecular genetics that allow us to understand the singularities of local populations in a zonal context, behavioral ecological studies that have made it possible to deepen our understanding of intra-population phenomena and their consequences such as parental care and dispersion, and the importance of puma predation on the guanaco, are highlighted.

8.4.1 Genetic Patterns of the Patagonian Guanacos in Chile

The evolutionary history of the guanaco in South America has increased notably thanks to advances in molecular genetics. Mitochondrial and nuclear DNA markers, including cytochrome b, d-loop, microsatellites, and genomic analysis, among others, have made it possible to answer questions related to delineation of the species, subspecies, populations, estimate demographic processes, and effective population sizes (Sarno et al. 2001; Marín et al. 2007, 2013; Casey et al. 2019; Varas et al. 2020; Fan et al. 2020); all of which potentially apply to guanaco management and conservation genetics (Marín et al. 2009; González et al. 2020; Mesas et al. 2021a). The current guanacos that inhabit Patagonia and Tierra del Fuego have been specifically studied to elucidate their past and recent history (Sarno et al. 2001; Bustamante et al. 2002; Maté et al. 2005; González et al. 2014; Mesas et al. 2021b, Table 8.5).

Currently it is possible to characterize two periods of guanaco occupation of Patagonia, especially where fossil DNA has generated relevant information. The first corresponds to populations of the "Pleistocene guanaco", whose records date between 13,275 and 10,630 years ago (Metcalf et al. 2016), which would have become extinct at the end of the Pleistocene along with most of the Patagonia megafauna. What is interesting about this group is that it occupies a unique and separate phylogenetic clade from contemporary guanacos, making the Pleistocene guanaco a distinctive polyphyletic group of the past (Metcalf et al. 2016; Moscardi et al. 2020). The extinction of this clade would imply a loss in the mitochondrial genetic diversity of the species, which surprisingly showed higher diversity rates than contemporary Patagonian guanacos (Moscardi et al. 2020). These antecedents cast doubt on what has been argued that the guanaco would have been one of the species that survived the mega-extinction of mammals in Patagonia since they would also have been affected (Markgraf 1985). The causes of such extinction of the fauna of that period are the subject of research and debate, posing various hypotheses, including climate change and the arrival of human populations to the region (Barnosky and Lindsey 2010).

The second period corresponds to an expansion of populations of new guanaco genotypes from the north that would have colonized Patagonia during the Holocene.

Table 8.5 Main genetic diversity indices (mean ± standard deviation) in guanaco obtained by mitochondrial and microsatellite markers in different Chilean localities in Patagonia

Locality (Latitude)	Number of haplotypes (gene name)	Number of private haplotypes	haplotype diversity	Mean number of alleles per locus	Observed heterozygosity	Genetical population (Marín et al., 2013)	Source
Valle Chacabuco (47°36′ S)	10 (d-loop)	6 (d-loop)	0.80 ± 0.09	6.33 ± 2.50	0.63 ± 0.16	Western Patagonia	González et al. (2014)
Torres del Paine (51°03′ S)	5 (d-loop)	2 (d-loop)	0.81 ± 0.05	6.75 ± 3.28	0.62 ± 0.19	Southern Patagonia	González et al. (2014)
	10 (cyt b)	8 (cyt b)	0.89 ± 0.03	7.60 ± 0.84	0.68 ± 0.40		Sarno et al. (2001)
Pali-Ayke (52°06′ S)	6 (d-loop)	1 (d-loop)	0.73 ± 0.09	6.75 ± 2.77	0.69 ± 0.13	Southern Patagonia	González et al. (2014)
Tierra del Fuego Island (53°18′ S)	4 (d-loop)	2 (d-loop)	0.36 ± 0.13	4.42 ± 1.98	0.50 ± 0.20	Fuegian zone	González et al. (2014)
	4 (d-loop)	–	0.56 ± 0.03	–	–		Barreta et al. (2013)
	4 (cyt b)	–	0.58 ± 0.05	–	–		Sarno et al. (2001)
	5 (cyt b)	3 (cyt b)	0.48 ± 0.10	4.70 ± 0.71	0.54 ± 0.59		
Navarino Island (67°15′ S)	3 (d-loop)	1 (d-loop)	0.46 ± 0.20	6.00 ± 2.30	0.30 ± 0.05	Not assigned	González (unpublished data)

These populations, dating 9730 years ago, would have managed to extend their distribution to Isla Grande de Tierra del Fuego and Isla Navarino, with estimated arrival dates of 8000 years and 6000 years, respectively (Sarno et al. 2001; Tivoli and Zangrando 2011). This advance to the South would have also fostered human expansion toward the Southern part of the continent (Rindel et al. 2020). The current genetic pattern of guanacos indicates that it is a monophyletic group, with its basal portion more phylogenetically structured (González et al. 2006; Marín et al. 2008) with the existence of two large-scale subspecies and population structure throughout its range of distribution in South America (Marín et al. 2013): *L. g. cacsilensis* inhabits the arid zone of the northwest of its distribution in the deserts and western slopes of the Andes of Peru and Chile, and shows at least two demographically independent populations with high levels of genetic diversity (Casey et al. 2019). On the other hand, *L. g. guanicoe* extends from Bolivia and northern Argentina to the southern tip of South America, where five genetic populations are found (Marín et al. 2013).

In the Chilean Patagonia at least three populations have been identified with population dynamics independent of each other. The populations correspond to those located in Western Patagonia, Southern Patagonia, and Fuegian zone (Marín et al. 2013). This differentiation on a population scale is defined by the levels of structuring inferred by genetic Structure (Fst). Guanacos of Isla Grande de Tierra del Fuego show a clear pattern of population structure when contrasted with continental populations that vary between 0.10 and 0.19. These values are high compared to localities in continental Patagonia, which vary between 0.05 and 0.11 (Sarno et al. 2001; Marín et al. 2013; González et al. 2014). Along with this, the mitochondrial and nuclear genetic diversity of Tierra del Fuego guanacos are low compared to the entire area, only surpassed by indices obtained in Isla Navarino.

These demographically independent guanaco populations generate restrictions on their management, which should consider their genetic makeup (Marín et al. 2013). Tierra del Fuego, due to its condition of island and isolation from the continent thousands of years ago, contains a population subject to selection pressures different from those of the continent that could be impacting its genetic identity, opening up new questions on the variation of functional genes (Fan et al. 2020).

8.4.2 Patterns of Maternal Expenditure in Juvenile Guanaco's Influence on Reproduction and Survival

The guanaco juvenile stage exerts a critical influence on individuals as adults; behavior (offspring and mother), body condition, population density, and climate interact to influence future survival and reproductive success of adult guanacos.

Chulengos (juvenile guanacos between birth and 1-year of age) are born after an 11.5-month gestation period. Adult females produce a single offspring that weighs about 10% of the mother's weight (Sarno and Franklin 1999). In fact, the estimated level of reproductive effort (birth weight$^{0.75}$/maternal weight$^{0.75}$) of guanacos falls within the range of species showing no differential energy expenditure on sons or daughters. In general, births occur during the day in the Chilean Patagonia; 78% of chulengos are born between 10:00 and 14:00 h (Franklin and Johnson 1994). Birthing time is likely under selective pressure so that newborns can dry off during the warmer mid-day temperatures. This same phenomenon is observed also in vicuñas (Franklin 1983). The pulse of births for 2–3 weeks in November and December is also an antipredator strategy, in which an abundance of prey exists for pumas during a short period of time (Franklin et al. 1999). In this way, the probability of any one chulengo succumbing to puma predation is reduced.

Birthweight of *chulengos* varies between 7 and 15 kg (Franklin and Johnson 1994). While birthweight of juvenile males and females is not different (12.9 kg, $n = 411$ Torres del Paine National Park), mean cohort birthweight displays a strong negative correlation with population density ($r = -0.871$, $p = 0.011$, $N = 7$) (Sarno and Franklin 1999). Since low birthweight (<10 kg) is associated with increased mortality (Gustafson et al. 1998), random fluctuations in population density likely influence chulengo survival. Furthermore, winter is challenging for chulengos. Therefore, forage intake of chulengos begins between 2 and 4 weeks of age. The response is an elevated growth rate during the first month of life with weight gain decreasing over time up to the following spring.

For several years, newborn chulengos were captured and tagged in order to understand patterns and causes of mortality and learn about other critical aspects of their life history. Aggression by adult females toward researchers during capture of newborns for tagging (a form of Maternal Expenditure = ME) increased offspring survival; these data demonstrated the range of behaviors by mothers toward members of the tagging crews – as far as we could determine – that were viewed as predators of their young. This behavior by mothers was crucial to the survival of their young. In fact, a 1-unit increase in maternal aggression (toward taggers) decreased the risk of chulengo mortality prior to dispersal by almost 24%. Therefore, adult female aggression toward researchers may reflect a mother's ability to protect and defend her offspring during its first year of life. Individual and random variation in components of ME clearly influence juvenile survival. While aggressive mothers appeared to increase the probability of chulengo survival during the period of parental care, increased winter snowfall (and population density – see above) tended to decrease it. For each 1 cm of snowfall, the likelihood of chulengo mortality increased by about 6% (Sarno et al. 1999).

Mean juvenile survival rate (S′) was 0.38 but varied between 0.31 and 0.55. Survival rates between the sexes were not significantly different, although male survival was lower than that of females. Mortality rate was highest during the first 14 days after birth. Most deaths occurred between birth and 7 months of age. Puma predation was the leading cause of mortality in all years, followed by unknown disease, and miscellaneous causes (Sarno et al. 1999).

Chulengos remain with their mothers until approximately 1 year of age and during this time interaction between chulengos and territorial males (even though they might be related) are rare. During spring, however, territorial male guanacos become increasingly aggressive toward juveniles born the previous birth season and begin expelling them from their territories. Aggression from territorial males is overt, intense, and potentially injurious to juveniles. In an apparent effort to deter adult male aggression, juveniles display "submissive crouches" when near adult males – even as far as 40–50 m away. The submissive crouch is an obvious and apparent subordinate behavior in which juveniles lower their long necks toward the ground, raise their tails, and bend their knees; this posture mimics that of a nursing juvenile (Franklin 1983; Sarno et al. 2003).

Although juvenile males are generally forced to disperse earlier than juvenile females, the proportion of dispersing males ($n = 49$) and females ($n = 46$) is similar ($P > 0.05$). Because of variation in the timing of forced dispersal, juveniles can be classified into one of three dispersal categories: early (below the median expulsion date of 6 December), late (after the median expulsion date), or delayed (after 31 December). Early-dispersing individuals are significantly younger than late dispersers ($\bar{x}$=349 vs. 381 days), and nearly 2 months younger than delayed-dispersing animals. The mean number of submissive crouches/hr. of early dispersers and delayed dispersers ((1.20, 1.42, and 2.63, respectively) was not significantly different ($P > 0.05$). However, the rate of submissive crouches by delayed dispersers was nearly 75% higher than early dispersing animals. These data tend to support previous work (Lorenz 1966; Koutnik 1980; York and Rowell 1988) demonstrating that juvenile subordinate behavior reduces aggression from adults. Submissive crouches by juvenile guanacos may also promote familiarity among unrelated conspecifics (Bernstein 1964, 1969; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1985; Reynierse 1971; Poole 1973). Ultimately, the forced dispersal of juvenile guanacos by territorial males appears driven by feeding competition.

Although delayed-dispersing animals receive extended maternal care, the benefits of delayed dispersal are enigmatic, because there is no relationship between the timing of dispersal and survival until 4 years of age for either sex. In contrast, reproductive performance up to 4 years of age for males but not females are inversely associated with dispersal time: the longer juveniles remained in family groups prior to dispersal, the less likely they would reproduce as adults.

8.4.3 The Puma as a Population Modulator of Guanacos in Torres del Paine National Park, an Historical Perspective

The Patagonia puma (*Puma concolor patagonica*) has been the primary and only predator on the guanaco. Their coexistence has shaped the behavior, habitat selection, and birthing pulse of the guanaco (Franklin et al. 1999; Sarno et al. 1999; Bank et al. 2003, Chap. 4).

Intensive studies were conducted at Torres del Paine National Park (1981–1995) of the puma-guanaco interaction. Methodology included puma scat analysis, guanaco skull collection, puma radio collaring, and newborn chulengo tagging and radio collaring (Iriarte et al. 1991; Franklin et al. 1999; Sarno et al. 1999). Research was centered in a 200-km^2 core study area located in the center of the park where 90% of the park's guanacos were in 4000 ha (Ortega and Franklin, 1988).

Pumas were occasionally seen in the early 1980s, but sightings increased dramatically in the mid- to late 1980s. Between 1986 and 1989, 13 pumas were equipped with radio transmitters. During the winter of 1988, there was one puma per 17 km^2 in the 200 km^2 study area. Home ranges varied from 24 to 107 km^2. Female home ranges overlapped with males and other females extensively, but male ranges overlapped with each other for only short time periods. Seven adult pumas had home ranges extending outside the park boundaries and at least three preyed on sheep (Franklin et al. 1999).

Puma sightings continued to increase into the early 1990s with 3 to 14 sightings per year. In the mid-1990s, puma sightings numbered 20–50 per year (Franklin et al. 1999). Observations from highly experienced field workers identified a total of 12 Pumas including five kittens in the 40 km^2 study area, equivalent to 30 pumas/100 km^2 or 17.5/100 km^2 not including kittens (Bank and Franklin 1998). Since first reporting such high densities, other authors have questioned how these estimates were determined (e.g., Walker and Novaro 2009). Nevertheless, puma abundance could be explained by the increase in the guanaco population. From 1975 to 1988 the guanaco population in the study area increased 13-fold from 97 to 1276 animals.

Early puma food habits revealed that European hares (*Lepus europaeus*) were the most numerous prey of pumas (Iriarte et al. 1991), but in terms of biomass guanacos (59%) were the most important food source. Yet, European hares were preyed on more and guanacos less than expected relative to their estimated biomass availability in the Peninsula. In the area of high guanaco density, pumas fed on an estimated 13 European hares for every one guanaco. As both the puma and guanaco populations increased, so did the impact on guanacos: frequency of guanaco remains in puma scats increased from 9 to 29% between 1982–1983 and 1987–1988 (Iriarte et al. 1991; Franklin et al. 1999). Based on the field-guanaco skull collection (1979–1988, $n = 731$), 33% of the skulls showed distinct evidence of having been killed by pumas. More were killed in winter and spring (63%) and in areas of high guanaco density with almost equal numbers of both sexes (49% males, 51% females, $n = 70$ skulls). Fifty-nine percent of the skulls were chulengos and yearlings (1–12 months old). Relative to their availability, chulengos were preyed upon about four times as much as adults. The estimate of one-third of the guanaco skulls of all age classes were from individuals killed by pumas was suspected to be low because skulls of the first year-age class are often broken up and scattered during consumption. Pumas often kill guanacos by a bite to the throat, leaving the skull undamaged. In addition, skulls of young animals were more problematic to locate in the field since they can be easily broken, eaten, and carcasses covered by plant debris and/or scattered. It should also be noted that in contrast to North America where pumas show a preference for adult ungulates (see Hornocker and Negri 2010), pumas in Torres del Paine selectively preyed on chulengos.

To better understand puma impact on chulengos the survival of 409 radio-collared newborns with motion-mortality sensors from 1991 to 1995 was assessed. Puma predation was the main cause of chulengo mortality. The mean yearly survival rate of chulengos in the early 1990s was 38% (i.e., 62% mortality) (Sarno et al. 1999), lower survival than based upon life table analyses in the early 1980s (Franklin and Fritz 1991; Fritz and Franklin 1994) and substantially lower from mark-resighting studies in the late 1980s (Behl 1992) that had a mean yearly survival of 70% (i.e., 30% mortality). Predation was the leading cause of radioed-chulengo mortality in the early 1900s: puma 79% (76–83%), unknown 14% (5–20%), miscellaneous 6% (2–13%), and disease 1% (0–5%). Chulengo mortality was especially high in 1991 (67%), 1993 (69%), and 1994 (68%). We suspect that the dramatic increase in chulengo mortality from the 1980s compared to the 1990s was due to the unusually high density of pumas.

Mortality was highest in the first 14 days after birth when 23% of all radio-collared chulengos died. In the first year, all chulengo deaths occurred in the first 120 days. While puma predation was the most important cause of first-year deaths, winter conditions were believed to have been a predisposing factor to predation. Mean monthly winter snowfall increased the risk of chulengo mortality by 5–7% for each additional centimeter of snow (Sarno et al. 1999; Franklin 2011).

Thus, puma mortality on a guanaco population can be highly significant when nearly 70% of young of the year are lost primarily to puma predation. When additional annual mortality is added over the next several years, guanaco cohorts suffering high chulengo mortality would eventually contribute very little to population growth by the time they become reproductively mature. Puma-caused mortality at this level can have a severe modulating or even regulating impact on a guanaco population.

8.5 Guanaco Conservation Strategies in Chile

Historically, two major strategies have allowed the recovery of guanacos in the Chilean Patagonia over the last six decades, both have been applied as a broad policy at the national level. First was protective legislation, which prohibited hunting of the species, and second the establishment of large territorial spaces that gave protection to small populations of guanacos, but allowed their growth sheltered from the negative factors that caused the species to disappear, specifically hunting.

8.5.1 Chilean Legislation Applied to Guanaco Protection and Management

Legislation on fauna in Chile began with the publication of the Civil Code in 1888, that defined fauna as "wild, domestic and domesticated" species, and established the domain of wild animals acquired by occupation, among others. The publication of Law No. 4.601 on Hunting in 1929 represented the first specific legislation on wildlife and was in force for 67 years until 1996. It declared that guanaco hunting was prohibited for 3 years. In 1929 the capture and sale of guanaco newborns was prohibited as well as, the exportation of guanaco hides and skins were taxed at one dollar per gross kg, and established penalties for violators of the law. In 1993 when Law DS-133 was published, a ban for conservation purposes for a period of 20 years was made official for the guanaco. Then in 1998 with publication of DS-05, guanaco hunting was prohibited throughout the nation.

Current national regulations state that the guanaco is a protected species, with a permanent hunting ban due to "reduced population densities" on a national scale. The hunting regulations classified the guanaco in the "Endangered" category in the North, Central, and South Zones of the country, and "Vulnerable" in the Austral Zone (DS-05/1998), later specifying for Magallanes as "Out of Danger" (DS 65/2015). In 1989 "The Red Book of the Terrestrial Vertebrates of Chile" had also classified the guanaco in far southern Chile as "Out of Danger". Finally, the Regulation for the Classification of Species into Threatened Categories, created by the Ministry of the Environment, classified guanaco as "Least Concern" in the southern part of Chile (Fifth Species Classification Process, May-2010). This classification made it possible to apply the criteria of the IUCN Red List at a regional scale.

At the international level, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), signed by Chile through DL No. 873 of 1975 and applied by Law 20.962 of 2016, classified the guanaco in Appendix II, which allowed for the commercial export of guanacos and their products with prior authorization from the Administrative and Scientific Authority of Chile. Without prejudice to the permanent prohibition of hunting throughout, the regulations empower SAG to authorize on an exceptional basis, quotas for the capture of live animals or their hunting when the objective is for the formation of reproduction centers, hatcheries, or research purposes or the sustainable use of the species.

Complementing the general rule, the Ministry of Agriculture established a technical policy for guanaco management in Tierra del Fuego in 1998, allowing for the harvest of surplus populations in the south-central area of the island of Tierra del Fuego. This latter ruling was necessary for the sustainable management within these ecosystems. This was later extended to the north of the island in 2009 and to the mainland of this district in 2016. Currently, guanaco is hunted under the control of the Agricultural and Livestock Service only in the Magallanes district (see section Management based on hunting).

Table 8.6 Main protected areas in Chilean Patagonia containing guanaco populations

Protected area name (Administrative district)	Creation date	Surface (ha)	Guanaco population	Main ecoregion available	References
Cerro Castillo N. R. (Aysén)	1970	179,600	20	Magallanes sub-polar forest	Cunazza (1991)
Patagonia N.P. (Aysén)	2018	304,527	2800–3200	Patagonian steppe	González and Acebes (2016)
Torres del Paine N.P. (Magallanes)	1959	181,400	2500	Patagonian steppe	This chapter
Pali-Aike N.P. (Magallanes)	1970	50,300	245	Patagonian steppe	SAG 2021
Karukinka Park (Magallanes)	2004	270,000	10,000–15,000	Magallanes sub-polar forest	Based in Moraga et al. (2015)
Yengegaia Park (Magallanes)	2013	150,612	No information	Magallanes sub-polar forest	
Total		1,136,439			

8.5.2 Protected Areas in Chilean Patagonia, Refuges for the Guanaco

The protected wild areas in Chile have been, together with the supporting legislation, one of the major guanaco protection actions taken for the Chilean Patagonia (Table 8.6). The protected areas were part of a network of wild areas that historically belonged to the State and administered by the National Forestry Corporation, to which primarily private lands were later added, doubling the total protected areas for guanacos (González et al. 2013).

Some of the best examples of protected areas that have given protection to small populations of guanacos throughout the country include: Pan de Azúcar National Park, Llullaillaco National Park, Río Cipreses National Reserve, and the Pali-Aike National Reserve (Cunazza et al. 1995). Other wild areas, mainly in Patagonia, have seen a significant increase in the number of guanacos, such as the Torres del Paine National Park (Sarno and Franklin 1999) and the recent Patagonia National Park in the Aysen district, which are formed by the union of the Jeinimeni and Lago Cochrane National Reserves to the former Hacienda Chacabuco, the latter donated by the Tomkins Conservation Foundation in 2017. In addition, there was the creation of a protected area in southern Tierra del Fuego by the Wildlife Conservation Society called Karukinka in 2004 of 2700 km^2, that has expanded the protection in grassland-forest ecotone environments, prime habitat for guanacos.

8.6 Guanaco and Livestock Interactions

Ecological interactions between species could become conflicts when different human interests collide. If conflict is not managed or transformed to coexistence, the problem can become a threat to the species and its ecosystem. This situation has occurred in much of the distribution of the guanaco in Patagonia where the interests of traditional livestock production conflict with the interests of protection of this species. Here two interactions are analyzed: one spatial in the surroundings of Torres del Paine National Park, the other trophic between sheep and guanaco. Finally, the interaction is analyzed from the social perceptions of the actors who coexist in the territory.

8.6.1 Spatial Competition in Agrarian Areas around Torres del Paine National Park

The recovery of guanaco populations in protected areas of Magallanes during the last decades has led to the progressive occupation of neighboring areas devoted to livestock grazing, as explained in the section of population trends above. Such recolonization of areas formerly occupied by the species gives rise to a new situation of potential for competition with domestic ungulates, a case of interest on the grounds of theoretical ecology and with potential socioeconomic impacts for the agrarian sector of the district. The effects of guanaco recent colonization on livestock production will depend on a combination of wild and domestic species' densities in the new areas, and as competition theory postulates, their actual spatial overlap. Again, the case of Torres del Paine area is where more research on the subject has been developed where the guanaco populations coincided with domestic ungulates in a pattern that can be depicted as a wave expanding away from the original core populations of the species in the protected area of a national park.

From a theoretical point of view, guanaco expansion should begin with the dispersal of juveniles away from protected areas where the species reaches high densities (Fretwell 1972). If conditions allow for it, dispersing individuals may set in the colonized area first followed by the establishment of new reproductive groups. Effective colonization then progressively leads to a dilution of differences in density, social structure, and/or demographic parameters with respect to the original populations (Darmon et al. 2007). In Torres del Paine area, censuses carried out from vehicles along 2009–2011 showed that the colonization process was already effective by 2010 though patterns revealed in the recent colonization process that was still detectable in a 25–30 km buffer around Torres del Paine National Park (Iranzo et al. 2018a). At that moment, the total abundance of guanacos outside the protected area more than doubles those inside it, with a gradient of decreasing density of ca. 25 individuals/km^2 in the western section of the park to 10–12 individuals/km^2 outside the park. Animal density varied among ranches depending mainly on their distance to the protected area but also on their topography, vegetation cover, and management.

The guanaco population was already firmly established in the livestock ranching area, and it showed demographic parameters very close to those estimated for the protected area. However, it was still possible to detect some differences in social structure, outstandingly a 54% higher frequency of male groups and a 43% lower frequency of solitary males in the recently colonized area. Here, family groups were also 19% more frequent, and all these features pointed to a younger and expanding population occupying the area. The reproductive parameters of guanaco in the surroundings of the national park were very close to those within it, with a chulengo/adult ratio of 0.32 that was just slightly higher than the one within the protected area. In summary, at present the guanaco population living outside the protected area has been settled there for more than a decade, and showing potential to produce an excess of individuals, thus allowing further increase in numbers and the colonization over a larger area of Magallanes as an expanding wave.

Under these circumstances, research carried out on landscape and habitat selection at a fine scale by guanacos and domestic ungulates is of special interest due to the potential presence of stress points with high and constant densities of the wild herbivore sympatric with livestock. Extensive data on habitat availability and use of space by guanaco and sheep gathered along the summers and winters of 2009 and 2010 allowed the analysis of topographical features and vegetation cover of sites effectively occupied by animals, and their comparison at a 50 m scale between species with availability estimated in control sites (Iranzo et al. 2013).

This approach evidenced a differential use of the agrarian landscapes. Sheep behaved as a generalist herbivore using different patches of the area according to availability, regardless of physiography or vegetation cover. On the contrary, guanaco selected hillsides and locations with wide visibility of the surroundings and preferentially grazed vegas and open areas with abundant bare soil and vegetation of cushion-like shrubs. Guanaco also avoided locations with denser vegetation and/or rugged terrain with lower visibility and potential higher predation risk by puma (Iranzo et al. 2013, 2018b). A similar situation was later described for the overlap in space use between guanaco and cattle in the same area (Traba et al. 2017). As a result, the potential for competition between guanaco and livestock was lower than the direct output of computations on herbivore densities and their fodder requirements.

The point here was that even though wild and domestic ungulates co-occur at the landscape scale, their overlap in use of space was at a lower spatial scale significantly lower than expected. Iranzo et al. (2013) also showed that guanacos selected the same landscape features both with and in the absence of livestock. This fact precluded the possibility that habitat segregation of guanaco and sheep in agrarian areas was the result of human activities (e.g., active harassing) in those places mainly devoted to livestock grazing.

However, these results did not confirm an absolute lack of competition between guanaco and sheep in the use of space, as demonstrated by a refined re-analysis of these data together with those corresponding to a third sampling year (Traba et al.

2017). Thus, the quantitative analysis of niche use corroborated the presence of significant differences in space use by guanaco and domestic ungulates, but also a significant over 40% overlap among them. Moreover, interspecific effects were detected in niche utilization of both sheep and guanaco: the local abundance of each species reflected on the effective niche of the other, leading to some niche compression that fits with predictions in the case of interspecific competition (Chase and Leibold 2003). Also, such trace of competition was stronger in winter coinciding with the season of greater food shortage, which alerts about the presence of subtler effects or of limitations in the spatial overlap of both species in the most stressful situations. Unfortunately, the lower number of livestock observations precluded a parallel analysis for this case.

It is important to note that the area surrounding Torres del Paine has a high heterogeneity in climatic conditions and physiography (Luebert and Pliscoff 2006) that are directly mirrored in the landscape features selected by guanacos that must be extrapolated to other areas in Patagonia. Strong altitudinal and rain gradients associated with the proximity to the Andes, together with human activities have generated very diverse habitats in this area in terms of slope-valley gradients and areas covered by grass, scrubs, or woods that compose the frame for the differential habitat selection by guanaco and livestock. In large sectors of the Patagonian steppe such possibilities for habitat differentiation may be scarce and spatial competition between herbivores may be stronger. Finally, all these analyses are focused on the spatial arrangement of herbivores where they co-exist that should be complemented with data on the actual consumption of different plant species by ungulates to have a clear picture of the potential for competition between them.

8.6.2 Competition for Food Resources in the Chilean Patagonia

Competition between wildlife and livestock is mostly related to two main ecosystem services, food production and biodiversity, giving a better understanding of the ecological interactions between domestic and wild ungulates as needed to maintain resource sustainability (Ranglack et al. 2015). Nonetheless, an increasing use of rangelands for livestock raising has had negative effects on plant diversity and production because of habitat degradation through overgrazing and erosion (Ren et al. 2015). Under these circumstances, large wild herbivores are seen as competitors for livestock and detrimental for animal production activities (Gordon 2018).

Since the establishment of conservation plans to recover guanaco populations in the 1970s (Franklin et al. 1997), these efforts have resulted in an increase of guanaco population across its range, especially in Patagonia (Iranzo et al. 2013; Zubillaga et al. 2014a, b; Moraga et al. 2015). Due to this population increment, guanacos are currently relying on private lands predominantly committed to sheep ranching (Baldi et al. 2004; Iranzo et al. 2013; Moraga et al. 2015). Public claims by ranchers point out that guanaco population levels are extremely high (Moraga et al. 2015; Hernández et al. 2017), which if true would substantially reduce forage availability for sheep, together with grassland deterioration (Oliva et al. 2019). However, rancher's statements have been stated as controversial because sheep stocking densities appear to exceed carrying capacity of Patagonian arid steppe based upon widespread range deterioration (Marino et al. 2020; Castellaro et al. 2016). See also Chap. 3.

The most common approach to assess competition between livestock and wild ungulates is the determination of diet similarities and preferences (Arsenault and Owen-Smith 2002; Odadi et al. 2007, 2011), while the overlap of dietary vegetation items consumed by co-occurring species is the dominating study path on competition (Odadi et al. 2011; Butt and Turner 2012). Guanacos do not differ from this pattern since most of the knowledge about trophic interaction with domestic sheep is based upon diet overlaps (e.g., Baldi et al. 2001, 2004; Pontigo et al. 2020). Guanaco and sheep diets include the most available plant species of steppe-graminoids (Poaceae), nongraminoid herbs (Rosaceae and Fabaceae), small shrubs (Berberidinae and Apiaceae), and large shrubs (Astaraceae and Vebenaceae) (Puig et al. 2001; Baldi et al. 2004; Pontigo et al. 2020). However, both ungulates' diets are dominated by a few plant items, around 20% of consumed species (Baldi et al. 2004; Pontigo et al. 2020). However, both ungulates' diets are dominated by few plant items, around 20% of consumed species (Baldi et al. 2004; Pontigo et al. 2020).

Similarities between guanaco and sheep consumed food items are high (Puig et al. 2001: 0.82; Baldi et al. 2004: 0.93; Pontigo et al. 2020: 0.97), which has been explained by similar selection strategies of both species (Baldi et al. 2001, 2004; Pontigo et al. 2020). These similarities in feeding strategies and selection between sheep and guanaco would promote competition in periods and habitats where food resources are scarce (Baldi et al. 2004; Pontigo et al. 2020). However, guanacos have low metabolism rates allowing them to survive in rough environmental conditions (Van Saun 2006), as well as being opportunistic and generalist herbivores that can inhabit different environmental conditions from mountain areas and forests to arid steppes (Franklin 1983; González et al. 2006). This camelid can digest substandard vegetation and feeds on a wide variety of plant species (Linares et al. 2010). Although sheep are also considered generalist herbivores with medium selectivity (Ginane et al. 2015), they have larger metabolic rates, so they need better forage conditions than guanacos to survive (Van Saun 2006).

Despite trophic resources used between guanaco and sheep are highly similar (Puig et al. 2001; Baldi et al. 2004; Pontigo et al. 2020), to assess competition requires additional variables (Butt and Turner 2012) such as the foraging distribution of guanaco and sheep in areas of co-grazing or in single species grazing areas (Iranzo et al. 2013; Traba et al. 2017), and differences in use of foraging resources accordingly to their metabolic needs (du Toit 2011). Small herbivores need high-quality forage to fulfill their nutritional requirements, while large herbivores achieve their needs through a generalist diet favoring quantity instead of quality (Demment and Van Soest 1985).

Although the dietary overlap of guanaco and sheep has been reported, there are insufficient data on the availability of plant food in the grasslands (Hernández et al. 2017; Pedrana et al. 2019), but the impact of sheep on vegetation seems to be greater than guanaco, mostly because different feeding strategies and the number of animals present (Pedrana et al. 2019; Pontigo et al. 2020). Pontigo et al. (2020) argued that guanacos currently cope with sheep competition because of their adaptability and tolerance to inadequate environmental conditions, while sheep out-compete guanaco through exploitation using most of the food resources because of their large numbers and human support. Sheep have shown low variation in their trophic niche when co-grazing with guanaco, while guanaco significantly reduces their trophic niche when co-grazing with sheep, suggesting that guanaco is affected by sheep unidirectionally (Pontigo et al. 2020).

Guanaco distribution and habitat use have been modified across Patagonian steppe by sheep ranching activities and structures, even after land use activities have been terminated (Antún and Baldi 2020). Sheep overgrazing has been the major force modifying sparse-grassland ecosystems throughout all Patagonia steppe, considering that >95% of the land is privately owned (Baldi et al. 2004; Antún and Baldi 2020). This environmental degradation has due to overgrazing led to controversies about the implication of both ungulate species' role in the steppe recovery (Oliva et al. 2019; Marino et al. 2020). Changes in economic interest on sheep products and steppe degradation have declined the number of sheep because damaged grasslands cannot support former past numbers of sheep ranching (Baldi et al. 2004).

8.6.3 Interactions Between Guanacos and Livestock Ranching: Social Perceptions, Local Conflicts, and Potential Solutions

Conflicts between the interests of livestock production and those of wild-herbivore conservation are globally increasing, thus becoming challenging. Wild herbivores can potentially compete with livestock for resources, whose interactions often lead to exacerbated wildlife-human conflicts even when it is not clear if competition occurs (Pozo et al. 2021). In such circumstances, ranchers may persuade authorities toward the control of wild populations to diminish the conflict. On occasions, wild herbivores are persecuted, contributing to their on-going global decline.

This is the case of Chilean Patagonian rangelands, where traditional sheep livestock production has been the primary land-use and the major economic income in the region since sheep introduction at the end of the nineteenth century. Until then, guanacos were the only ungulate inhabiting Patagonia since the end of the Pleistocene some 10,000–12,000 years ago. The increase in sheep stocking rates, peaking in the 1950, brought a steady decline of pastures' production due to poor management practices that triggered soil degradation (Golluscio et al. 1998; Chartier and Rostagno 2006). This situation led to a progressive decline of sheep numbers. In parallel, guanacos were perceived as competitors, persecuted, and their populations drastically declined. In summary, social conflicts between the wild herbivore and livestock production were the main cause and the most important obstacle to guanaco conservation. In the early 1990s the guanaco was included in Appendix II of the CITES Convention (1992), which restricted its trade and required a series of conservation measures for the species. These actions, together with the abandonment of ranches and the creation of several protected areas, such as Torres del Paine National Park (TPNP), contributed to the guanaco recovery, even reaching high population densities in some areas. Accordingly, social conflicts between ranchers and local authorities have rekindled.

A study conducted in Magallanes district about rancher perception on guanaco-livestock conflicts stated that livestock stocking rate was the most critical factor impacting rangelands, and that intensive management practices had contributed to pasture deterioration (Hernández et al. 2017). However, ranchers considered that guanaco competed with livestock for forage, thus limiting livestock production. Most ranchers identified guanaco overabundance as the main cause of conflict with livestock. Interestingly, they considered the guanaco as an important component of their ecosystem, which provided them services beyond grazing. Ranchers noted that guanaco should be conserved but managed in cases of overabundance (Hernández et al. 2017).

Another study analyzing social conflicts between wild herbivores and livestock in the surroundings TPNP came to similar conclusions (Iranzo et al. 2015). Here, the guanaco population increased significantly in the last 40 years, spreading into the nearby ranches (Iranzo et al. 2017). Habitat selection and space use studies revealed moderate niche overlap between guanacos and sheep (Iranzo et al. 2013; Traba et al. 2017), despite having similar diets (Baldi et al. 2004; Pontigo et al. 2020). Still, ranchers perceived the guanaco as a disruptive element of their production systems for several reasons: its presence, population abundance and recent increase, the forage competition with sheep and as an attractor of pumas, that may eventually predate on their livestock (Iranzo et al. 2015; Kusler et al. 2017). These authors found a high abundance of guanacos nearby TPNP, although variable among ranches. Differences between local guanaco abundance and rancher perceptions would suggest that it is necessary to work on the social attitudes of the conflict to reconcile guanaco conservation and livestock production (Hernández et al. 2017; Pozo et al. 2021). Despite this, 65% of the ranchers were willing to assume some level of economic losses for the presence of wildlife in their ranches (Iranzo et al. 2015).

With this scenario in mind, the Chilean government authorized in 2000 the implementation of a plan for guanaco management in Tierra del Fuego. After no private interest for live capture of guanaco for captive initiatives or guanaco translocation for conservation purposes, the Chilean government authorized the commercial guanaco harvesting aiming to sustainable regulate guanaco populations while contributing with new products to the local economy (Soto et al. 2018). However, it was difficult to evaluate whether this plan succeeded in ameliorating the conflict

(Hernández et al. 2017). More local experiences of guanaco harvesting in the surroundings of TPNP took place for 2 years with limited results. In other parts of Patagonia, wild guanacos have been live-sheared by local communities for fiber production, with positive results in terms of people engagement, tolerance to guanacos and economic incomes, and animal welfare considerations (Montes et al. 2006; Taraborelli et al. 2017, see Chap. 7); nevertheless, continuity of the activity depends on the value of products in the market. Another promising measure to mitigate these conflicts is to offer farmers the opportunity to certify the guanaco products (meat, fiber) for the application of good environmental and sustainable practices on their ranches (WCS 2014). By developing these environmentally friendly practices, farmers obtain added value for their products. This is especially interesting in areas surrounding protected areas, such as the TPNP, which are increasingly receiving national and international tourism. One step beyond for ranchers is to host tourism in their ranches, as it is in fact already happening, which is especially welcome for tourists if they can watch wild fauna in their rangelands. That topic was also discussed by Franklin et al. (1999). Anyhow, approaches that balance traditional uses and modern conservation objectives, seeking to reconcile livestock production and wild herbivore conservation, are highly needed (Pozo et al. 2021). These approaches further need to incorporate different stakeholders in the search for agreed solutions.

8.7 Productive Management of the Guanaco, Failures and Successes

Consumptive management to obtain products has been the primary and traditional way of valuing the guanaco. This approach has been promoted by the Chilean national government through research and supported projects for the development of fiber and meat production. The approach for these two primary products was through two management modalities, captivity and hunting. However, not all programs have managed to go from the experimental to productive stage.

8.7.1 Management Based on Captivity

The keeping of guanacos in captivity is an activity that comes from pre-Columbian cultures. The objectives of keeping captive animals were varied, from obtaining assets to using them as pets. Possibly the “Chilihueque”, a camelid described by ancient chroniclers was apparently a tamed guanaco that was handled and used by the cultures of South-Central Chile (Benavente 1985; Wheeler 1995). In addition, there are photographic records that show the maintenance of tamed chulengos by some indigenous ethnic groups in Patagonia, since this animal was essential for the subsistence of these groups (Bridges 1948; Miller 1980). In the eighteenth century, the great Chilean naturalist Abate Molina (1788) mentions the presence of captive guanacos that had been easily "domesticated" Darwin (1839) observed the same in Northern Patagonia and reached the same conclusion.

A captive breeding of guanacos from 1987 to 2000 in Southern Chile was substantially funded and focused on primarily obtaining fiber and secondarily meat. The objective was guanaco production as an alternative to traditional livestock, imitating the experience of Argentina that had already conducted such research (Sarasqueta and de Lamo 1995). The first attempts at guanaco captive breeding resulted in low success due to the lack of fundamental knowledge of the biology and behavior of the species regarding individual and social adaptation to captivity. Seed stock for the captive guanaco farms was obtained as newborn chulengos and subadults; first attempts of raising newborns proved to be highly unsuccessful (Bas et al. 1995; Latorre 1999).

Six farms were registered with productive purposes, four located in the Magallanes district (see Table 8.7) which managed ca. 500 guanacos (Bas and González 2000). At present, all these facilities have ceased their functions, have been converted or have been closed. Despite great state and private effort, it was not possible to scale the farms from experimental initiative to commercial success mainly due to the high investment required and poor development of the guanaco fiber market. However, the technique developed in these captive experiments proved to be useful for other purposes, mainly that applied to ex situ conservation or rehabilitation techniques (Bas and González 2000; González et al. 2004).

Table 8.7 Summary of the main farms who managed guanacos in captivity in Chilean Patagonia

Farm name	Las Charas ranch	Lolita ranch	Olga Sofía – Bahía Lee ranch	CRI – Kampenaike ranch
Place and location	Magallanes district	Magallanes district	Magallanes district	Magallanes district
	Patagonian zone	Patagonian zone	Patagonian zone	Patagonian zone
Start date	1987	1991	1996	1997
Initial state subsidy	No	Yes	Yes	Yes
Production system	Farming (experimental)	Farming (experimental)	Ranching (experimental)	Farming (experimental)
Source of founders (type of animals)	Tierra del Fuego (new-born animals)	Tierra del Fuego (new-born animals)	Tierra del Fuego (family groups)	Tierra del Fuego (new-born animals)
Date of capture	1987	1991–1994	1996–1997	1997–1999
Initial aim	Hybridization with alpacas (not done)	Research & Production	Research & Production	Research & Fiber production
Current situation	Closed	Without management	Not in function	Closed

Data from Bas and González (2000)

8.7.2 Management Based on Hunting

The recovery of the guanaco population of Tierra del Fuego Island led to a state policy in 1998 that was intended to promote the sustainable use of the local population through the capture of animals and commercial hunting, prioritizing their live capture to establish a viable population in other areas of the country. However, there were no applicants for live captures for relocations and several for hunting. Similar technical criteria were applied when management of the populations on the rest of the island and on the mainland were established in 2009 and 2016, respectively. These include harvest quotas that are granted to the interested parties after studying the proposed harvest plan. The competent authority (SAG) authorizes the harvest quotas based on the information provided by the applicant and the results of yearly official population estimates. Generally, only harvest of less than 4% of the estimated population size for the year are approved (Soto et al. 2018).

The harvest includes field dressing, storage, and transport and concludes with slaughter in an industrial plant. The process is strictly supervised by officials of the SAG Agricultural and Livestock Service with permanent supervision in the field and in the plant. This is done between the months of June and August. Hunting is carried out exclusively on private properties with the proper authorization of the owner and is not permitted within 4 km of protected wild areas of the State or within 20 km of the border with the Argentine Republic when the meat is destined for foreign export. Hunting of young or female with young is prohibited, but otherwise does not distinguish between sexes. Hunters work in groups of two using large game firearms (cal. 308) with a telescopic sight from 4x4 vehicles on side (interior) roads. More than 80% of the shots hit the head of the animals, ensuring a rapid death and then efficient bleeding.

In the Magallanes district, from 2003 to 2019, permits were issued to harvest 42,250 guanacos, of which 79% (33,362 animals) were taken, producing 708,180 kg of meat, 1242 hides, and 18.85 kg of fiber that were exported under CITES authorizations. Approximately 538,000 kg of meat and bones were sold in the national market (SAG 2021). At present guanaco meat prices in the national market vary roughly between $7900 and $19,900 Chilean Pesos a kilogram (equivalent to $9.8 to $24.68 USD, March 2022) depending on the cut (Emporio Austral 2022).

Currently, the harvest of guanacos has begun to decline, in spite of a well-established and organized system with annual quotas, harvest by professional teams, on-site auditing by government personnel from the hunting sites to the cold storage plant, and meat ~~is~~ sold as frozen and portioned in local markets and exported under CITES permits. In recent years, the hunting quotas authorized by the SAG have not been covered, probably because of changes in demand in the destination markets. If the marketing problems of the harvest products persist, the guanaco will once again conflict with the livestock and forestry activities. This means that new and/or complementary alternative uses for its conservation must be looking for or developing.

8.7.3 Future Perspectives

Most information about Patagonian guanacos in Chile has been generated in the district of Magallanes. The recent establishment of new protected areas in the district of Aysen offers an opportunity for developing research protocols that would replicate and build on many of the topics that we have summarized here, including the estimation and monitoring of guanaco population size, guanaco interactions with native herbivores, and guanaco interaction with livestock in the surrounding areas. Since guanaco populations are shared between the Chilean and the Argentinean Patagonia, studies on animal movements and/or migrations are also needed for support transboundary conservation strategies.

An additional strategy for enhancing guanaco conservation focusing on the sustainable use of consumptive and non-consumptive products and services from the recovered populations is growing in popularity. This strategy includes controlled hunting and tourism. Hunting is restricted to the Magallanes district and is managed by private companies under the full supervision of the Agricultural and Livestock Service. Tourism is continuing to grow in the Magallanes district, mainly in Torres del Paine National Park where several neighboring private ranches are including activities that have reduced or complemented traditional livestock ranching. Land management approaches that focus on sustainable use and that value wildlife species are likely to help reduce antagonism against guanacos.

Conflict management requires a socioecological approach where decision-making is complemented by bottom-up approaches that include ranchers and others who interact with guanaco populations and their ecosystems. Currently, the top-down approach has been applied to management of the guanaco as part of the sustainable use of the species, where legislation identifies governmental agencies to promote and control the guanaco use.

Finally, future research is needed to elucidate more clearly the consequences of the interaction between livestock and guanaco, i.e., the competition for forage to examine putative feeding competition between guanacos and sheep under controlled studies using exclosures, and to know about diseases transmission among species on shared lands.

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Chapter 9
Lessons for the Future of Conservation and Sustainable Use of Guanacos

Gabriela Lichtenstein and Pablo Carmanchahi

9.1 Introduction

Social-ecological systems (SES) are those that include social (human) and ecological (biophysical) sub-systems in two-way feedback interactions. The term refers to intertwined people-environment systems and to emphasize the interdependent and co-evolutionary nature of these "coupled" interactions (Berkes and Folke 1998). One of the most relevant contributions of this book is its social-ecological approach, and that it seeks to cross-disciplinary barriers and boundaries, and integrate various branches of biology and veterinary medicine with archaeological and anthropological information. Such an approach provides a holistic view of guanaco conservation and use as a complex, multidimensional, and multi-scale process that is strongly impacted by the historical, political, and social context.

The social-historical, economic, and environmental processes that took place in Patagonia over millennia shaped the relationship between human communities and

G. Lichtenstein (✉)
Instituto Nacional de Antropología y Pensamiento Latinoamericano (INAPL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad de Buenos Aires (UBA), Buenos Aires, Argentina

IUCN SSC South American Camelid Specialist Group (GECS), San Martín de los Andes, Neuquén, Argentina

P. Carmanchahi
IUCN SSC South American Camelid Specialist Group (GECS), Buenos Aires, Argentina

Grupo de Investigación en Ecofisiología de Fauna Silvestre (GIEFAS), Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue (UNCO), San Martín de los Andes, Neuquén, Argentina
e-mail: pablocarman@comahue-conicet.gob.ar

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_9

guanaco populations. This relationship was originally in the form of a dependency of the original peoples on this species (Chap. 2), sometimes expressed as a two-way or reciprocal relationship. But after the Conquest of the "Desert",[1] the bonds between the animals and people were broken. This led to a "decoupling" of the social subsystem from the ecological subsystem SES,[2] and the loss of stewardship traditions that maintained the relationship.

The disarticulation of the indigenous way of life at the end of the nineteenth century was the turning point in human-guanaco-environment interaction in Patagonia (Chaps. 2 and 6). As mentioned in previous chapters, local inhabitants were killed and replaced by European settlers, and their knowledge was also "replaced" by that of new settlers that had a different rationale and approach for exploiting the environment. Traditional management gave way to European farming, and native species were replaced by imported domestic species. The policies of appropriation and re-distribution of land, added to the unwise application of a productive model designed for wetter ecosystems that did not include the use of native species (nor local knowledge), contributed along the years to desertification and thus to increase the conflict between producers and guanacos (Coronato 2010; Chap. 6).

The eradication process, which was also suffered by predators (Chap. 5), resulted in a population decrease of guanacos to 26% of their original range (Baldi et al. 2016). This reduction was so severe that it required national as well as international conservation efforts (such as export bans on guanaco pelts by CITES), and the elaboration of specific regulations for guanaco conservation (Chaps. 6 and 7). Meanwhile, desertification increased and became probably the most important social, economic, and ecological problem in Patagonia (Chap. 2). The climate crisis, in addition to poor livestock practices and overstocking for decades, led to the degradation of grasslands, which, combined with the crisis of the sheep wool market and the eruption of the Hudson volcano, resulted in a progressive abandonment of ranches particularly in Santa Cruz and Chubut provinces (Andrade 2003). This in turn benefited puma and guanaco populations, reigniting the conflict with remaining sheep ranchers (Chaps. 5 and 6).

In spite of public and private efforts to establish guanaco sustainable use projects and the solid science behind them (Chap. 7), there is a growing conflict between sheep ranching and guanaco conservation in most of Patagonia. Ranchers of Santa Cruz and Chubut provinces in Argentina, and Chilean Patagonia, are concerned about the recovery of some guanaco populations, which are perceived as uncontrolled and over the carrying capacity, leading to competition for forage resources with livestock and causing overgrazing and habitat deterioration, and

[1] The so-called Conquest of the "Desert" was carried out in 1879 in Argentina under the military command of Julio A. Roca, who was minister of war at the time. He organized a military offensive to put an end to the "problem" posed by the native peoples who were preventing him seizing full control of the territories to the south of the Colorado River.

[2] We borrow the term "decoupling" from Hoole and Berkes (2010), to mean the separation of the communities from their traditional territory, the "decoupling" or alienation of people from their local environment and their cultural heritage.

decreasing rangelands' receptivity (Chaps. 3 and 8). Lobbying by large-scale ranchers from Santa Cruz province resulted in permits to harvest 6000 guanacos and the update of the Guanaco National Management Plan. This non-participatory process was led by livestock sectors without knowledge about wildlife ecology and management (Chaps. 6 and 7).

However, the role of guanacos in the desertification process is debatable. Schroeder et al. in their review (Chap. 3) found no ecological evidence to support the idea that guanaco reduces forage availability for livestock through competition, nor that guanaco populations threaten rangeland integrity and livestock production through overgrazing. Furthermore, they documented a systematic underestimation of the environmental carrying capacity for guanacos when estimated by methods used for livestock, which impacts directly on the overgrazing risk assessment and calculation of harvest quotas.

This chapter summarizes some of the findings with policy impact mentioned in this book and draws lessons and opportunities for the conservation and sustainable use of the guanacos in Patagonia.

9.2 Lessons Learned and Opportunities for Guanaco Conservation and Sustainable Use

9.2.1 Nature Conservation Is a Highly Political Process

Nature conservation entails power struggles between the actors that participate in the definition and implementation of policies and power asymmetries. The perceptions and values of local communities and rural inhabitants are usually silenced in favour of influential actors such as ranchers and interest groups as illustrated in Chap. 6. The concentration of decision-making power in distant cities alienates local people from their natural resources. It is important to acknowledge the different agendas, and multiplicity of interests and values involved in decision-making.

9.2.2 Guanaco Conservation Requires Integrating Scientific Information from Disparate Disciplines as well as Local Traditional Knowledge into Decision-Making and Strengthening Participatory Processes

Guanaco conservation and management requires an integrated approach that includes research across a wide range of academic and applied disciplines for decision-making. Furthermore, management plans cannot rely only on "expert knowledge". Problem definitions are contextual and should be drawn from both local and scientific knowledge (Wilkinson et al. 2007). As mentioned in Chap. 3, planning, design, and implementation of management schemes affecting guanaco populations require strengthening participatory processes involving all relevant stakeholders (i.e., ranchers, pastoralists, indigenous peoples, scientists, conservationists, and policymakers). Such schemes should have an adaptive management (learning-by-doing) approach and knowledge co-production (combining different kinds of knowledge for problem-solving) (Berkes 2017). They should include transparent co-participation in the follow-up, monitoring, and evaluation of processes, as well as the horizontal transmission of management results among stakeholders. Failed programs and policies (such as the Pilot Programme to harvest guanacos in Santa Cruz, Chap. 6) should be terminated but lessons should be extracted and disseminated.

Government agencies should promote cooperation through programmes that strengthen the institutional capacities of wildlife and livestock managers as well as local participation. As may be observed along these pages, there is ample solid research tradition in Argentina and Chile, on different technical aspects of guanaco conservation and sustainable use. There are also on-going local experiences on collective guanaco management (Lichtenstein and Carmanchahi 2012) and some local indigenous knowledge on the relationship between guanacos and people that survived the colonization and dispossession process. As well, there are ancestral practices that need to be revitalized (Chap. 2, Dreidemie 2018). This book illustrates how the lack of participation of the academic sector, indigenous and local communities, and most provincial wildlife agencies in the updating of the guanaco management plan led to a mismatch between on-going development projects, local needs, scientific findings, and the regulations that were approved (Chap. 6).

9.2.3 The Implementation of Animal Welfare Protocols Based on Sound Science Is Crucial to Achieve Guanaco Sustainable Use

In the last 20 years, diverse aspects of the effects of live shearing guanacos have been studied. The response of wild guanacos to capture and shearing on physiological, behavioural, and population parameters was widely examined (Chap. 7). The outcomes of this research were incorporated into animal welfare protocols such as the IUCN SSC GECS (Carmanchahi and Marull 2017). The implementation of animal welfare protocols reduced the mortality and stress associated with shearing and thus the impact of live-shearing activities on population structure and fitness. Society's views on animal welfare have evolved over the past decades. Care for animal welfare criteria and good practices throughout the guanaco value chain are fundamental on ethical grounds and in the face of the growing pressure from international markets, animal rights campaigners, and NGOs. The challenge is to make sure that Animal Welfare Protocols are widely and properly applied in all shearing experiences. The fibre obtained from live animals following strict animal welfare protocols has the potential to be certified in a way that increases its sale value. On the other hand, fibre obtained from slaughtered individuals should not enter the market for the following reasons: (1) it is unfair competition for the on-going live shearing experiences; (2) difficulties in traceability might result in "laundering" illegal fibre, and (3) public concern on animal welfare might result in closing international markets for guanaco fibre (as it already occurred when the Patagonia firm stopped buying OVIS 21 wool).

9.2.4 A Transparent Market for Guanaco Fibre Should Be Established and Added Value at the Local Level Should Be Promoted

The rationale behind guanaco sustainable use experiences is that by allowing the commercial utilization of fibre obtained from live-shorn individuals, the development of positive local attitudes towards conservation would be encouraged. In turn, this should result in some or all of the following: a decrease in poaching; the replacement of introduced livestock with guanacos; an increase in tolerance for guanacos on private lands; better management of total grazing pressure; reduced land degradation; improving vegetation and biodiversity outcomes; and greater support for conservation measures (Lichtenstein 2013).

Although guanaco fibre has been exported for a long time to Europe, it is not as well-known as vicuña fibre. A lower international demand, the lack of an established and transparent market, and low market prices have all discouraged producers. In many areas, this results in poaching instead of legal use. Guanaco fibre has minimal differences from vicuña fibre, both are of excellent quality. However, guanaco fibre is not as recognized internationally (Kasterine and Lichtenstein 2018). Therefore, for the species to benefit in terms of conservation, guanaco fibre must be marketed as such. For this, it is necessary to establish marketing strategies that generate a demand for this product and ensure that this material comes from legal sources, certifying its traceability.

In addition, it is important to add value locally, avoiding the export of raw fibre for processing abroad. The use of ancestral practices for spinning and weaving guanaco fibre can re-invigorate local traditional knowledge and conserve cultural heritage while providing local economic benefits (Dreidemie 2018). Each of the fibre processing stages that is carried out locally not only increases the value of the final product, but also generates jobs and income for local communities, strengthening the links between people and the species, promoting recoupling.

9.2.5 Harvesting Guanacos for Meat Requires Filling Information Gaps

In various chapters of this book, it has been clearly shown that there are still large information gaps in relation to the production and marketing of guanaco meat (Chaps. 4 and 8). From the population point of view, the current harvest models are highly criticized by the scientific sector and require revision. From a regulatory point of view, it is important to establish control protocols and traceability of meat. From a health point of view, the high incidence of sarcocystosis is a problem that must be studied to establish whether it is feasible to market this product (Chaps. 4 and 7). On the other hand, the market for the products obtained by the consumptive use of the species needs to be made transparent in order to determine costs, profit margins, the destination of these products and their potential consumers. As in the case of kangaroo management in Australia, harvesting programs should be based on well-designed harvesting models and marketing, promoting sustainable population management. This should include selective harvesting based on sex, size, and age class (Finalyson et al. 2021), and this is very different from the untargeted culling/killing practices actually in place in Argentina.

9.2.6 The Uncertainty Regarding Resource Rights Over Guanacos and the Unequal Distribution of Usufruct Rights Reduces the Likelihood of Producers Becoming Interested in Joining the Activity and Instead Promotes Poaching

Guanacos share with other common pool resources (commons) that they are natural goods characterized by the difficulty of excluding actors from using them and the fact that their use by one individual or group means that less is available for others, known as the exclusion problem and the subtractability problem, respectively (Ostrom 1990; Ostrom et al. 1999).

Commons scholars have shown how, by shaping the incentives of users and managers, variations in forms of property rights make a difference in resource management outcomes (Agrawal 2003). In the case of guanaco management, there is a tension given that the resource is *de jure* (by law) state-owned, but exists as de facto (in practice) private property (Chap. 6). This results in ranch owners managing guanacos almost as private property. Public ownership of a resource that is scattered either in protected areas or on private properties across an area the size of Patagonia creates open access conditions that result in poaching instead of sustainable use. The uncertainty regarding resource rights over guanacos, and the top-down approach followed during the development and implementation of Management Plans should be re-visited in order to increase participation. There is a need to revise management strategies and create cross-scale interactions and partnerships as well as local-level common property institutions to decentralize the governance of this resource. Guanaco management provides an opportunity to target usufruct rights towards indigenous and local communities.

9.2.7 Need for Governmental Support at Different Levels

Producers venture into guanaco fibre production at their own risk. National and provincial governments provide limited investment or technical support. The design of local institutions for resource management has not been promoted. Ironically, there are more support schemes for sheep ranching (despite the desertification that results from overstocking) than for guanaco. Guanaco Management should be implemented not only by the Federal Biodiversity Agency (FBA). Strong participation of the State is still necessary, both in the control of the productive processes and in the development and marketing of products. In this sense, the participation of different official agencies related to the promotion of micro-enterprises through accessible credits, support in social organization and training, the promotion of internal and external trade, the generation of markets and the development of standards of market-driven production quality. Policies and regulations that facilitate (and do not inhibit) the access of indigenous people and cooperatives to guanaco management and the market should be encouraged.

9.2.8 Need for Work on Policies at a Regional Scale

Guanaco movements transcend political and administrative boundaries and therefore their use and management requires cross-boundary cooperation and coordination. Policies should result from agreements at different levels, cutting across the jurisdictional scale (vertically) and linking decision-makers at the same level (horizontally) (Berkes 2017). In the case of the international level, guanaco conservation would benefit from the existence of a Convention (such as the Vicuña Convention) where countries in its area of distribution can discuss and agree on conservation measures, share failed and successful experiences, technical knowledge and information.

9.3 Recoupling the Social and the Biological Systems

Wildlife management on a landscape scale is often complex, particularly where different land use practices co-occur (Finlayson et al. 2021). It often results in conflicts between the needs of wildlife and human needs, which are the main source of threats to biological diversity in much of the world. Human pressure on the environment is leading to processes of extinction of wild species and degradation of native habitats. In arid Patagonia, more than 95% of the land is private property and was converted mainly to sheep farming, under a poorly planned scheme, with fixed livestock loads and without considering interannual fluctuations in primary (plant) productivity, which led to a process of severe habitat desertification and the decline of wild species, such as the guanaco (Chaps. 3 and 7). As mentioned, desertification is the main environmental problem in the arid zones of Patagonia, causing important impacts on the quality of life and economy of the people who live there.

The degradation of the productive system due to desertification generates permanent migratory flows of rural inhabitants towards urban centres. These migrations break down rural families, generate important cultural losses and, at the same time, increase poverty in urban centres. In this context, the use of guanacos may have a fundamental role in mitigating the desertification process of arid ecosystems, providing an economic alternative for local producers, and increasing the profitability of the land due to its aptitude for complementary or alternative uses (Lichtenstein and Carmanchahi 2012). The use of guanaco fibre could become an important complement to regional economies, transforming this activity into an engine for local socio-economic development, playing an important role in the conservation of the species.

The paradigm shift that favours the coexistence between the conservation of wild species and the productive activities of local communities is slowly taking root in society. This is because the value of biodiversity is being recognized on moral, ethical, and aesthetic grounds, as well as for recreational and economic reasons. Therefore, considering activities for the sustainable use of wildlife, which minimize environmental impacts and favour coexistence between production and conservation, will have positive consequences for ecosystems and biodiversity. Cultural and biological diversity and abundance of options, on the other hand, will increase the resilience of the social-ecological system and its ability to buffer or adapt to change (Berkes 2017).

We suggest that guanaco sustainable use is a way to recouple social-ecological systems in Patagonia to restore the cultural heritage of stewardship traditions, and to achieve habitat and species conservation. The on-going re-articulation process, contributing to revitalization, and updating of indigenous cultural references, identity affirmation, and rediscovery of local and community practices taking place in Argentina and Chile might contribute to this end (e.g. Pilquiman et al. 2020; Lichtenstein and Cowan Ross 2021) along with continuous work with ranchers.

It is time for policy-makers to start envisaging natural resource use and management holistically in terms of linked social-ecological systems, and to embrace transdisciplinary perspectives. This would hopefully be supported by reforms in university education fostering non-reductionist approaches to science (Schoon and Van der Leeuw 2015). A broader outlook should include the active participation of indigenous and local low-income communities that have been historically neglected in favour of large-scale producers. Such policy changes would create a more even "playing field" for guanacos and people.

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Correction to: Guanacos and People in Patagonia

Pablo Carmanchahi and Gabriela Lichtenstein

Correction to: P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*, Natural and Social Sciences of Patagonia, https://doi.org/10.1007/978-3-031-06656-6

This book was inadvertently published without box 3.3 in chapter 3. It had duplicated table headers within the table for tables 3.1 and 3.2. It should include box 3.3 within chapter 3.

In addition to this in chapter 7, a chapter call-out was incorrectly mentioned as chapter 2. It should read "Conflicts related to interspecific competition manifested through dietary overlap, diet shifts, and spatial segregation (see Chap. 3)".

The updated original version of this chapter can be found at
https://doi.org/10.1007/978-3-031-06656-6_3
https://doi.org/10.1007/978-3-031-06656-6_7

P. Carmanchahi, G. Lichtenstein (eds.), *Guanacos and People in Patagonia*,
Natural and Social Sciences of Patagonia,
https://doi.org/10.1007/978-3-031-06656-6_10