

A model for llama (*Lama glama* Linnaeus, 1758) domestication in the southern Andes

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ABSTRACT

The aim of this paper is to present a three-stage model that specifies the possible mechanisms for the domestication of the guanaco (*Lama guanicoe cacsilensis* Lönnberg, 1913), which gave origin to the llama (*Lama glama* Linnaeus, 1758). A more comprehensive analytical framework is proposed, beyond the wild-domestic dichotomy. The model takes into account the interaction of two components: animal and human behaviors. Simultaneously, we analyse the types of selection acting in the different stages of the domestication process and the archaeological evidence available.

KEY WORDS

Domestication,
South American
camelids,
Andes,
modeling.

RÉSUMÉ

Un modèle pour la domestication du llama (Lama glama Linnaeus, 1758) dans les Andes du sud.
L'objectif de ce travail est de présenter un modèle avec trois stades qui spécifient les possibles mécanismes de domestication du guanaco (*Lama guanicoe cacsilensis* Lönnberg, 1913), qui donna lieu à l'origine du lama (*Lama glama* Linnaeus, 1758). Nous proposons ici un cadre analytique plus explicite qui va au-delà de la dichotomie entre sauvage et domestique. Le modèle prend en compte l'interaction de deux facteurs tels que le comportement humain et le comportement animal. Nous analysons simultanément les types de sélection qui ont agi sur les différents stades du processus de domestication et l'évidence archéologique disponible.

MOTS CLÉS

Domestication,
camélidés sud-
américains,
Andes,
modélisation.

TABLE 1. — Sites, chronology, and cultural contexts in which the earlier evidence of llama-size or llamas have been determined by osteometry, allometry, and/or pathology. Llamas in sites below 3000 masl are dated later than 2000 years BP. This could represent the expansion of domesticated llamas from Puna to Mesothermal valleys.

Map number	Site	Altitude	Dates (BP)	Cultural Context	Reference
1	Hornillos 2	4050 m	6340-6190	Cave/domestic	Yacobaccio <i>et al.</i> (2013)
2	Alero Cuevas	4300 m	5106-4210	Cave/?	López (2012)
3	Tulán 52	3200 m	4500-3860	Village/domestic	Cartajena <i>et al.</i> (2007)
4	Puripica 1	3250 m	4800-4050	Village/domestic	Cartajena <i>et al.</i> (2007)
5	Inca Cueva 7	3650 m	4080-4030	Cave/cache/offering	Yacobaccio (2004)
6	Pozo Cavado	3700 m	3884±59	Cave/?	López (2012)
7	Alero Sin Cabeza	3672 m	3610-3390	Cave/domestic	Grant (2010)
8	Huachichocana III	3400 m	3400±100	Cave/burial	Yacobaccio & Madero (1992)
9	Alero Unquillar	3600 m	3550-3500	Rockshelter/domestic	Yacobaccio <i>et al.</i> (1997-98)
10	Tulán 54	3200 m	3080-2380	Village/domestic	Cartajena <i>et al.</i> (2007)
11	Cueva Quispe	4020 m	2472±33	Cave/domestic	Yacobaccio <i>et al.</i> (2011)
12	Casa Chávez M1	3450 m	2400-1300	Village/domestic	Olivera & Grant (2009)
13	Alero Huirunpure	4270 m	2040-1560	Rockshelter/midden	Yacobaccio <i>et al.</i> (1997-98)
14	Yutopián	3000 m	1630±60	Village/domestic	Izeta (2010)
15	Cardonal	3000 m	1878±57	Village/domestic	Scattolin (2006)
16	Loma Alta	3000 m	1600-1365	Village/domestic	Scattolin (2006)
17	Soria 2	1945 m	1940±80	Village/domestic	Belotti Lopez de Medina (2011)
18	Piedras Blancas	1040 m	1370-1000	Village/domestic	Dantas (2012)
19	La Rinconada	1100 m	1250-1220	Village/ritual	Svoboda & Eguia (2010)

INTRODUCTION

The domestication process is usually explained as a major transition in the evolution of human society (Boulliet 2005). Domestication is the result of the interaction between people and wildlife which entailing a change in the relations between society and nature, with two active actors involved. This exchange between two species implies that many of the actions taken by a species during its mutually adaptive relationship are a response to changes in the other species (human or animal). As stated by O'Connor "...the process of domestication is unlikely to have been one-sided [...] rather [it was] a particular interaction by behavioral adaptation on the part of both species [human and animal]" (O'Connor 1997: 152). Zeder considers domestication as a "biological mutualism" that benefits each partner in the association (Zeder 2012; Russell 2012: 206). The relationship between humans and animals is a complex one, and can be characterized in different ways; domestication is just one particular mode of human-animal interaction. Domesticatory relationships are part of a metasystem that brings together the cultural and ecological systems and their interactions and dynamics through time (Vigne *et al.* 2011: 255).

The contribution of this paper lies in its interdisciplinary approach that considers the biology of the animal undergoing a domestication process as an essential player. This kind of conceptual framework focused on the relationship between both species is applied here, for the first time, to the studies of the camelid domestication process carried in the Southern Andes during Mid-Holocene times (see also Yacobaccio & Vilá 2013).

In recent years, archaeozoological research in the Southern Andes has provided evidence to support the claim that a local process of camelid domestication took place in the Altiplano of this region (references included in Table 1). We can summarize this evidence as follows:

1. Appearance of llama-size individuals in several sites of the Puna de Atacama since 6200 BP (Table 1; Fig. 1).

2. Detection of pathologies indicative of captivity in several animal bones – especially feet bones, such as arthropathies, strangled marks, periostitis ossificans – since at least *c.* 4200 BP (Cartajena *et al.* 2007).

3. Appearance of naturalistic rock art depicting a relation of protection between people and camelids since 4000 BP (Taira-Tulán style [Gallardo 2009]; Río Punilla style [Aschero 2000]). Also, Sepúlveda *et al.* (2013) report naturalistic camelid paintings in the Arica range dated around 6000 BP to 3700 BP.

4. First occurrence of yards or corrals in caves or as stone structures built on the borders of peatlands in deep ravines, as early as 4100/3600 BP (Aldenderfer 1998; Aschero & Yacobaccio 1998; Cartajena *et al.* 2007).

5. Detection, through pollen analysis, of environmental anthropic impact attributable to environmental management practices (i.e. greater abundance of Chenopodiaceae-Amaranthaceae, Pennisetum) (Schäbitz *et al.* 2001; Oxman 2015, *c.* 4500 BP), suggesting more intensive human intervention to modify the natural landscape.

The entire camelid domestication process took a long time, during which a number of environmental and cultural changes occurred in the Puna or Altiplano between 3200 and 4500 masl (metres above sea level; Table 2). Since this process is a Mid-Holocene phenomenon, it must be considered in the context of the environmental change that took place during this period. The transition from Early to Mid-Holocene conditions, between 8200 to 7500 BP, is synchronous with the end of a humid phase known as the Coipasa event (Sylvestre *et al.* 1999). This marked a steady trend toward a more arid environment, which is indicated by the complete drying-out of some Puna lakes (Morales 2011). These long-term environmental changes increased spatial heterogeneity, which prompted new strategies and behavioral modifications

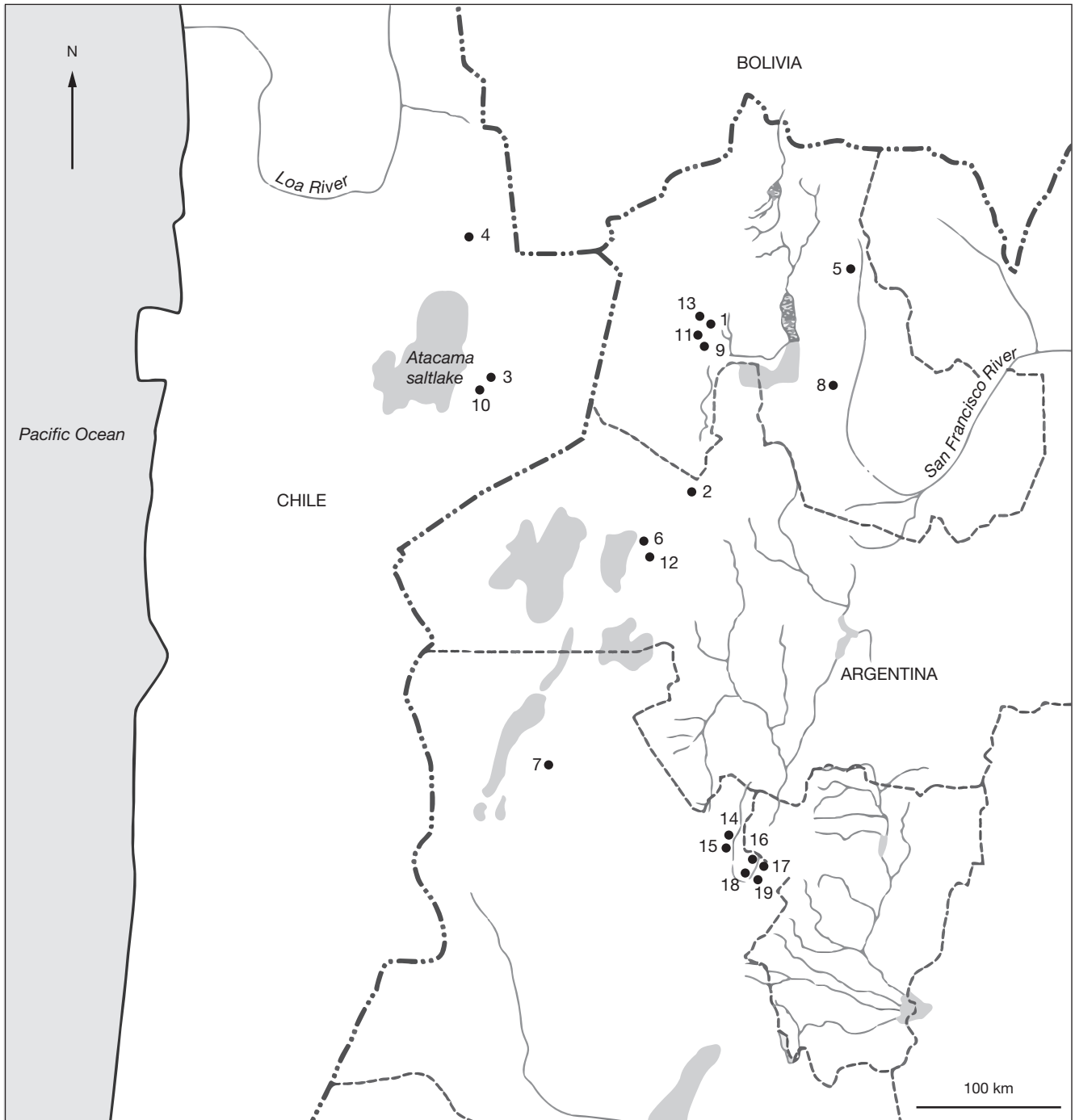


FIG. 1. — Map of Northwestern Argentina and Northern Chile showing the location of relevant sites. Puna sites: 1, Hornillos 2; 2, Alero Cuevas; 3, Tulán 52; 4, Puripica 1; 5, Inca Cueva 7; 6, Pozo Cavado; 7, Alero Sin Cabeza; 8, Huachichocana III; 9, Alero Unquillar; 10, Tulán 54; 11, Cueva Quispe; 12, Casa Chavez M1; 13, Alero Huirunpure. Mesothermal Valleys sites: 14, Yutopíán; 15, Cardonal; 16, Loma Alta; 17, Soria 2; 18, Piedras Blancas; 19, La Rinconada.

among human populations, such as increased technological diversity, a reduction of mobility, and, at the end of the period, the emergence of social complexity (Table 2). Environmental fragmentation became more severe *c.* 6200 BP, but resilient habitats seem to have been relatively stable in a centennial to millennial scale in certain localities, such as narrow ravines, upper river drainages, and wetlands, generally located above 4000 masl. These patchy habitats presented high vegetation

coverage and water availability, becoming relatively more productive in terms of resources relevant for human and wildlife populations. In these scenarios, innovations such as specialized hunting and protective herding emerged as viable strategies for coping with fragmented habitats (Yacobaccio 2013). Also, the fragmentation of the environment prompted a closer relationship between people and camelids, nucleating their populations in these patches.

TABLE 2. — Summary of the environmental and cultural characteristics by time-period. Abbreviation: **ENSO**, El Niño Southern Oscillation.

Period	Climate and Environment	Features of human occupation
Early Holocene (11 000-8200 BP) (12 890-9200 cal BP)	Stable, moist and cold Weak seasonality in precipitation Positive hydrological balance	Small occupations Low artifact diversity Low transport rates of artefacts between localities Opportunistic use of animal resources Residential mobility
Middle Holocene I (8200-6200 BP) (9200-7100 cal BP)	Arid and warm, marked seasonality in precipitation Fragmentation Negative hydrological balance Short term variations Long-term directional variation	More diversity of projectile points New hunting techniques Grinding tools Logistical mobility Specialization in animal use
Middle Holocene II (6200-3500 BP) (7100-3770 cal BP)	Extreme regional aridity Negative hydrological balance Fragmentation with habitat loss Short term incremental variation (first ENSO) Slightly more humid as from 4000 BP (4470 cal BP)	Subsistence diversification (camelid domestication and introduction of cultivated plants) Social complexity Reduction of mobility

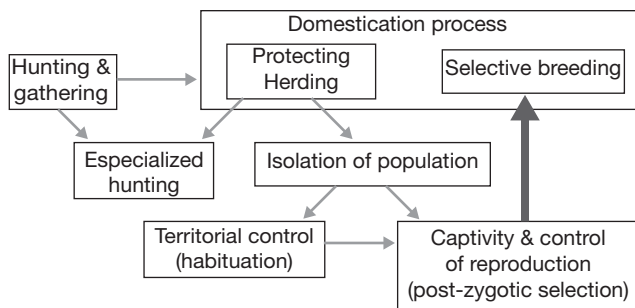


Fig. 2. — A three step model for llama (*Lama glama* Linnaeus, 1758) domestication.

The South American camelids are composed by two genera and four species, two wild (vicuñas *Vicugna vicugna* Molina, 1782, and guanacos *Lama guanicoe* Müller, 1776) and two domestic (llamas *Lama glama* Linnaeus, 1758 and alpacas *Lama Cuvier*, 1800 or *Vicugna pacos* Linnaeus, 1758). Vicuñas live only in high altitude Puna environments – i.e. above 3400 masl, from Peru to Argentina and Chile, between 9° and 29°S. This species lives in family groups composed by one male, three to four females and two offspring. These groups are stable and territorial all year round. The mating system has mixed components of polygyny, resource defense, and harem (females + calves) defense, because the alpha male limits and defends an area, but he also conducts the females to the territory when they move far away (Vilá 1999). Guanacos widespread throughout the Andean range from Peru to Tierra del Fuego from 8°S to 55°S, inhabiting a variety of open habitats (arid, semi-arid, hilly, mountain, steppe), and temperate forest environments (subpolar *Nothofagus* forest in Patagonia). There are two sub-species: the northern guanaco (*Lama guanicoe cacsilensis* Lönnberg, 1913), and the Patagonian guanaco (*Lama guanicoe guanicoe* Franklin 2011). Guanaco social structure in the breeding season comprises three basic social units: territorial family groups; male groups (non territorial), and solitary males (Franklin

1982). Territoriality in family groups is directly correlated with stable food supply. When a severe drop in food availability occurs, usually in the winter, guanaco populations move, losing territoriality, breaking apart family groups and forming mixed herds (Merino & Cajal 1993).

Genetic studies of living populations suggest that llamas descend from the northern guanaco, and the alpaca from the vicuña, with an early introgression with llama (Wheeler *et al.* 2006). Both wild species have a number of ecological and behavioral adaptations that are favorable for domestication (Driscoll *et al.* 2009), such as dominance hierarchy, persistent groups, male dominance over females, and taming potential. The model we discuss in this paper is mainly designed to establish the mechanisms of northern guanaco domestication, although we consider it to be potentially applicable to vicuñas as well.

THE MODEL

The process of domestication can be divided into stages, as has been observed by other scholars who proposed complex mechanisms for explaining domesticatory relationships *before* the generation of domestic breeds. For example, we can mention the incipient domestication stage (Kolska-Horwitz 1989) which is relevant to this discussion. Incipient domestication implies an increased level of contact and control between humans and animals preceding domestication, characterized by manipulation and selective breeding (Kolska-Horwitz 1989: 156-157). Zeder (2015) defined domestication as a “sustained relationship, in which one organism assumes a significant degree of influence over the reproduction and care of another organism”. This process includes a first step of “management” which is the manipulation of the conditions of growth of an organism, or the environment that sustains it.

The model that we present in this paper can be observed in Figure 2. It consists of three stages: the first one is generalized opportunistic hunting; the second is protecting herding

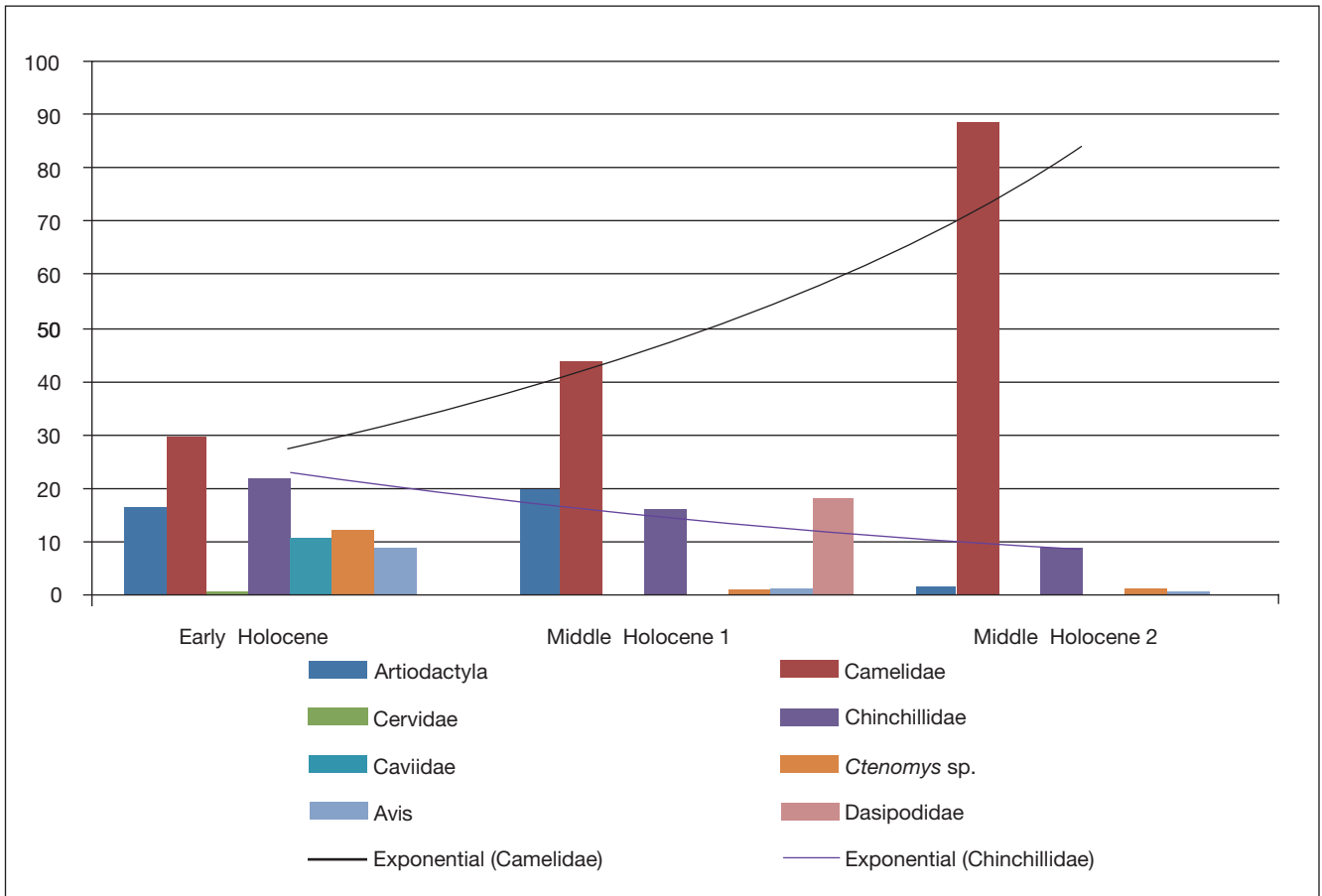


FIG. 3. — Representation of regional archaofaunas (% NISP), and time-trends for Camelidae, and Chinchillidae. Camelids increase over time, meanwhile the other animal resources diminishes.

(a concept similar to management), and the third, selective breeding. Both the second and third stages are part of the domestication process.

The archaeological evidence from the Early Holocene (10 000–8200 BP) indicates that hunter-gatherer groups were composed of small, highly mobile social units that used an extended area within a region that offered large productive patches. This favored a strategy that minimized transport of raw materials between locations, allowing occupational recurrence in certain localities (Aschero & Martinez 2001; Nunez *et al.* 2010; Morales 2011). This is observed also in the uneven distribution of the amount of camelid bone remains on a regional scale. Generally, the faunas of the Early Holocene were more diverse, and many localities have an abundance of small fauna, such as rodents, especially the viscacha (*Lagidium viscacia* Molina, 1782), birds, and *Xenarthra* (armadillos) (Fig. 3; Table 3).

Generally, hunting by small human groups has a mild impact on wild species, as it has little effect on the gene pool (Panter-Brick *et al.* 2001). Typically, the ungulate prey response to hunting is flight behavior (Stankowich 2008). The most common reaction towards human disturbance in wild ungulates is flight behavior, which is a sound, measurable proxy to evaluate population distress;

flight initiation distance – i.e. the distance between the predator (or the human disturbance or presence) and prey when the prey flees, the time to the first escape, and other metrics are accurate indicators of fear in animals (Miller *et al.* 2006), and are useful in the assessment of an animal's welfare state (Dwyer 2004). Many factors influence the decision to flee in animals, but flight decisions interrupt the animal's normal behavior. This behavior is disruptive, costly, increases the visibility of the performing animal and, in the long term, interferes with important aspects of reproduction (Stankowich 2008).

The second step of domestication is characterized by protective herding, and it was taken during the second half of the Mid-Holocene. This is a relationship based on human intervention in a guanaco population, or population sub-groups, whose individuals are protected from its non-human predators and are provided with facilitated access to feeding areas (Harris 1996). This strategy may be concomitant to specialized hunting on the protected animals. In the archaeological record, specialization is evidenced in the increase of the target population, together with a reduction of other faunal resources (Table 3; Fig. 3). We estimate that this stage took place from 6200 to 4000 years BP; the first appearance of corrals has been dated at the end of this period.

TABLE 3. — Taxa recorded (NISIP) from 28 sites and levels in the Puna of Atacama (Chile and Argentina) between 3200 and 4200 masl (data from Yacobaccio 2013: Tables 3, 4, 5).

Taxa	Early Holocene (10 000-8200 BP)	Middle Holocene 1 (8200-6200 BP)	Middle Holocene 2 (6200-3500 BP)
Artiodactyla	2142	1018	371
Camelidae	3868	2235	24837
Cervidae	73	10	0
Chinchillidae	2817	817	2355
Caviidae	1382	12	0
<i>Ctenomys</i> sp	1576	54	313
Aves	1149	51	133
Dasipodidae	10	924	0
Total	13017	5121	28009
N sites/levels	11	7	10

Protective herding implies the physical presence of humans close to the animals, in a frequent, non-aggressive behavior towards protected guanacos. As the frequency of this contact increases, habituation of the animals to human presence is very likely to occur. In early stages of this process, while hunting was simultaneous to protection behavior, the relationship between people and animals could have been very close and frequent, and probably very influenced by the guanaco behavior. At this time, a change in guanaco's perception about humans must have taken place; people must have changed its role from aversive stressors that trigger the flight response, to a non-aversive, neutral presence that generates habituation. Habituation is termed as "the simplest form of learning", it is well studied behaviorally, and implies a decrease in response strength (Thompson & Spencer 1966). The repeated application of a stimulus (in our model, human presence) results in a progressive decrease in a response parameter (in our model, guanaco flight behavior) to an asymptotic level. This change may include decreases in the frequency and/or magnitude of the response. As habituation is contextual and exhibits spontaneous recovery, the only way to maintain this behavior is by frequent encounters without aversive association.

Current studies about reactions of guanacos to people show that in preserved areas (like Torres del Paine in Chile), where people are mostly tourists, the guanacos showed habituation and closeness, and in areas where people usually approach guanacos aggressively (e.g., poaching), the guanacos showed flight response and aversive displays, and ran hundreds of meters away from the person (Zapata pers. comm. 2010).

A study that compares flight behavior in wild guanacos and vicuñas in areas with and without poaching, shows that in poaching areas, 70 % of the camelid groups reacted by running away following the detection of the vehicle, whereas only 30 % of groups took flight in the preserved areas. The response latency was also smaller in areas with frequent poaching (Donadio & Buskirk 2006). These studies demonstrate the guanacos' behavioral plasticity in relation to the same stimulus (human presence), which can trigger a flight reaction when it is associated with gun firing, thus becoming highly aversive, or can lead to habituation if it is presented in a context of neutrality.

The contextual scenario is crucial for understanding the relationship between people and guanacos in early stages of domestication. If people can protect the herd through frequent interaction with no aversive events, thus achieving habituation, then the habituated animals will be easier to hunt with bow and arrow or atlatl, if hunting is conducted with high efficiency and low impact (what currently is named "animal welfare").

Hunting with arrows can be very effective in killing the animal without triggering the flight among the remaining individuals in the group, as it is quick and stealthy. The behavioral attitude of hunters heavily influences the remaining guanacos, who can possibly maintain their habituation over the flight response. Referring to the Selk'nam of Tierra del Fuego, ethnographer Martin Gusinde (1982) stated that although they could hunt guanacos with guns, they preferred arrows because the gun shot noise frightened the remaining guanacos and made them more frightful and irritable, and therefore very difficult to hunt. Animals can easily de-habituate if a new stimulus occurs in the context where the habituation took place (Groves & Thompson 1970). Clearly, with the appropriate technique, specialized hunting can be conducted with little impact on the habituated population. Diverse morphologies of bifacial lanceolated projectile points were used at the time in which we infer protecting herding was in place. They decreased in size from 6000 to 4000 years BP, perhaps as a consequence of the gradual developing of a particular hunting strategy that did not require hunters to keep a long distance away from the prey (Restifo & Huguin 2012).

In the phase of habituation, people are a neutral stimulus. When people become a *positive* stimulus – usually associated with the presence of food or shelter – another kind of learning emerges: an associative one, which generates the taming process. Tameness is a condition for reproductive manipulation, and for the isolation of the population in confinement or captivity, which is the next step in the domestication process. This third step involves a greater degree of protection and isolation – meaning the existence of a physical barrier between wild and captive populations. The space constraint increases animal density, resulting in changes in the social structure. Bachelor males must be removed or separated because of the continuous fighting with other

males, thus the choice of mating partner is greatly restricted. There may be cases in which a strong artificial selection is absent in confined animals; natural selection in captivity could cause differential mortality and reproductive failure among artificially selected populations (Price 2002: 51; Marshall *et al.* 2014).

However, the captivity environment quickly imposes conditions – food security, reduction in competition for nutrients, absence of predators, higher population densities, genetic isolation – under which natural selection is reduced. Therefore, the domestic phenotype is shaped by conscious or unconscious human selection. Strong artificial selection (or “methodical” selection, Darwin 1868) is the production of economically distinct varieties. The generation of varieties of llamas known today (*karas*, *tampullis* and intermediates) is the consolidation of the final phase of domestication.

Our working hypothesis is summarized in Table 4; it associates the human and animal behavior with the type of selection acting during the domestication process. Protective herding is largely characterized by forms of unconscious selection allowed by the habituation of camelid populations. Unconscious selection is intended to naturally preserve the most valued individuals (Darwin 1868). Only with the intervention of humans in animal reproduction in the next stage, with confinement, artificial selection (or methodical selection, in Darwin’s terminology) becomes predominant, and the formation of animal breeds finally occurs. One of the main questions regarding guanaco domestication is why the domestication took place in the northern Andes of Argentina, Bolivia and Perú, which is inhabited by *L. g. cacsilensis*, and not in the Patagonian Andes, particularly since most of the Patagonian hunter-gatherers were dependent of the sub-species *L. g. guanicoe* as their main food resource (Miotti 2012). Again, the interdisciplinary approach that incorporates the guanacos as active players in the scenario can shed light on this issue.

Migration in guanacos today only occurs in preserved areas, but historical information suggests that migration was very common among guanaco populations in Patagonia. A recent paper on habitat use (Puig *et al.* 2011) states that guanacos conduct altitudinal migration, forced by the deep snow coverage. Taphonomical data demonstrates massive death events among guanacos due to winter stress (Belardi & Rindel 2008). Winter-associated mortality has been identified as an important cause of fluctuation in wild guanaco populations (Merino & Cajal 1993; Cajal & Ojeda 1994; Sarno 1999). Massive guanaco mortality is not uncommon in Patagonia, which has a pattern of heterogeneity and unpredictable climate factors. The Puna or Altiplano of the northern Andes has less snow than Patagonia, where the snow is an important environmental constraint to herbivore diets. One of the possible strategies to adapt to seasonal change in the availability of resources is migration (Fryxell & Sinclair 1988; Albon & Langbatn 1992). Migratory animals and the people that use them as a resource can only reach stages 1 and 2 of our domestication model, and only going to the extreme of following the animals throughout their migra-

TABLE 4. — Comparison between human and camelid behaviors in relation to the stages of the process, specifying the types of selection acting in each stage.

Human Behaviour	Camelid Behaviour	Type of Selection
Hunting-gathering Residential mobility	Flight Aversive	Natural
Specialized hunting Protecting Herding Logistical mobility	Habituation	Natural + Unconscious
Confinement (corrals) Sedentarism/ Seasonal mobility	Taming	Artificial (pre- & post-zygotic) + Natural

tion cycle. In this case, the domestication process does not conclude with artificial selection in order to select a change of the phenotype, although it does allow for habituation and the resulting facilitation of hunting. So, for both the animal and human populations, interactions could have been limited to protective herding; animal confinement and care, in particular locations, did not provide sensible advantages in the prevailing harsh and unpredictable weather conditions, which promoted the dispersion of human and camelid populations.

CONCLUSION

The transition between hunting and herding has been a complex one, meaning that we should not expect it to have been a straightforward process. In this paper we have proposed a model for llama domestication that includes three-steps: hunting-gathering, protecting herding, and selective breeding – confinement and taming. Protecting herding involves changes in camelid behavior and modifications in human strategies to approach wild camelids, and it lasted for a long time: 6200 BP to *c.* 4000 BP, when evidence of corrals first appear in the region. Environmental fragmentation promoted the aggregation of human population and wildlife in resilient habitats, thus creating the conditions for the development of a closer relationship between people and camelids. Then, as a condition for protective herding, human communities reduced their mobility, stabilizing their residence in these areas where resources were more concentrated.

The most prolonged human occupation of these resilient habitats was not due to the net abundance of resources, but to their concentration, as indicated by the paleoenvironmental evidence (Tchilinguirían & Morales 2013). In these places, sustained interactions between people and camelids developed within the framework of protection and habituation. From 4200 to 3800 years BP, this process intensified and concluded with the confinement of the protected population and operation of artificial selection, first by post-zygotic selection – i.e. selective culling, and later by pre-zygotic selection – where mates are chosen by humans (Driscoll *et al.* 2009; Zeder 2012). The intensification of these conditions, together with a reliance on the exploitation of domestic camelids, set the basis for later herding practices. Herding is an economic system

based on domestic animals that requires people to organize their settlement and mobility strategies, in order to suit the needs of their livestock (Butt 2010).

In this paper we have emphasized the mechanisms, environmental changes, human and animal behaviors that culminate in the domestication of protected animals. A thorough understanding of this process is of utmost importance to understand the more profound changes brought by the emergence of camelid pastoralism, which characterized high Andean civilizations.

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