

# Recurrent deaths of guanacos (Lama guanicoe) due to winter stress in Southern Patagonia: averaged samples and change of analysis scales

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### RECURRENT DEATHS OF GUANACOS (LAMA GUANICOE) DUE TO WINTER STRESS IN SOUTHERN PATAGONIA: AVERAGED SAMPLES AND CHANGE OF ANALYSIS SCALES

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Abstract. Actualistic taphonomic observations of guanaco carcasses resulting from two winter mass death events that occurred in 2020 and 2023 at various locations in the Coyle-Gallegos River interfluve (Santa Cruz, Argentina) provide valuable information about the formation of the fossil record. In this paper, we discuss how studying these die-offs allows us to monitor the formation of the so-called averaged samples. The longitudinal monitoring of carcass assemblages aggregated in different years forced us to change the scale of analysis, which gradually approached a controlled averaged sample. In this long-term study, we evaluate the main variables involved in the processes of guanaco carcass accumulation, such as the regularity and causes of massive accumulations, the locations of dead guanaco concentrations, the spatial superposition of deaths, and the variation in the size of bone patches due to processes such as carnivore action, trampling, and gravity sliding. For the analysis, we used the concepts of accumulation cycle, tempo, settling in, fossil stability, formational forcing, and retarding factors. Our results allow us to propose various conditions of bone preservation and identify spatial sectors with better burial opportunities, which are useful for constructing long-term viable analogous models, the usual ones of the archaeological and paleontological

Key words. Actualistic taphonomy. Bone accumulations. Massive deaths. Generic and specific redundancy. Settling in. Accumulation cycles. Patagonia.

Resumen. MUERTES RECURRENTES DE GUANACOS (LAMA GUANICOE) POR ESTRÉS INVERNAL EN EL SUR DE PATAGONIA: MUESTRAS PROMEDIADAS Y CAMBIO DE ESCALAS DE ANÁLISIS. Las observaciones tafonómicas actualistas de carcasas de guanacos resultantes de dos muertes invernales masivas ocurridas en los años 2020 y 2023 en una variedad de localizaciones en el interfluvio de los ríos Coyle-Gallegos (Santa Cruz, Argentina), ofrecen valiosa información acerca de la formación del registro fósil. En este trabajo discutimos cómo el estudio de estas muertes nos permite monitorear la formación de lo que se denominan muestras promediadas. El seguimiento longitudinal de conjuntos de carcasas que se agregaron en distintos años obligó a cambiar las escalas de los registros, los que fueron aproximándose a una muestra promediada controlada. En este estudio a largo plazo se evalúan las principales variables que intervienen en los procesos de acumulación de carcasas de guanacos, tales como la regularidad y las causas de las acumulaciones masivas, las localizaciones de las concentraciones de guanacos muertos, la superposición espacial de muertes y la variación en el tamaño de los parches óseos por procesos como la acción de carnívoros, el pisoteo y el deslizamiento por acción de la gravedad. Para el análisis empleamos los conceptos de ciclo de acumulación, tempo, settling in, estabilidad fósil, forzantes formacionales y factores retardatarios. Nuestros resultados permiten proponer diversas condiciones de preservación ósea e identificar sectores del espacio con mejores oportunidades de enterramiento, a fin de construir modelos análogos viables para escalas a largo plazo, las usuales del registro arqueológico y paleontológico.

Palabras clave. Tafonomía actualista. Acumulaciones óseas. Muertes masivas. Redundancia genérica y específica. Settling in. Ciclos de acumulación. Patagonia.



IN THIS PAPER, we will focus on methodological aspects of an actualistic study to discuss the criteria used in taphonomic and archaeological interpretations. Actualism refers to studying contemporary processes and their products to assign meaning to evidence from the past (Gifford-Gonzalez, 2018). Actualistic observations of guanaco (Lama guanicoe Müller, 1776) carcasses in the interfluve of the middle basins of the Coyle and Gallegos Rivers (Santa Cruz province, Argentina; Figs. 1.1-2) are used to evaluate archaeological cases, highlighting the need to address the mixing of bones from naturally deceased animals with archaeological materials (Borrero, 1988; Massigoge et al., 2015; Belardi et al., 2022, 2025). There is limited concrete information about the conditions and rhythms involved in the formation of surface bone palimpsests and their eventual preservation in stratigraphy. Natural causes of massive bone accumulations typically include winter stress and rapid cooling events, such as those examined here, although examples of this type of death are rare in the literature compared to deaths resulting from floods, sediment flows, droughts, bogging, trapping, or other phenomena (Behrensmeyer & Hook, 1992; Rogers & Kidwell, 2007).

We present the current status of a study on recurrent winter stress deaths of guanacos, which allows us to monitor the formation of bone assemblages that can be considered averaged. This case is particularly suitable for discussing the conditions under which modern bones are incorporated into the fossil record and create mixtures with archaeological materials (Belardi et al., 2025). Our survey began with observations in 2020 and systematic records from 2021 to the present. The deaths resulted from cold waves occurred during the winters of 2020 and 2023. Belardi et al. (2025) published detailed discussions of the 2020 mass accumulation in the different environments of the interfluve. According to the Río Gallegos airport weather station, which is the closest to the study area, in 2020, there were three cold waves, and in 2023, only one, whose duration in days was longer (6 days) than the longest event in 2020 (4 days). Additionally, the maximum and minimum temperatures of the 2023 cold wave were more severe, with a maximum of 0°C and a minimum of -14.7°C (Bonfili, 2024). As we will see below, these conditions intensely affected the guanaco population in the region.

## The interfluve of the middle basins of the Coyle and Gallegos Rivers

The steppe landscape between the Coyle and Gallegos Rivers was shaped by glacial action (Ercolano *et al.*, 2016). Consequently, erosion is more prevalent than deposition on the terraced plains, leading to limited soil development. The region experiences a cold temperate climate with an annual temperature range of 0°C to 12°C. Winters are cold to very cold, influenced by polar and subpolar winds, resulting in substantial snow accumulation (Oliva *et al.*, 2001).

A characteristic of the region is the prevailing westerly winds, with an average speed of 4.6 m/s and a maximum speed of 360 m/s (Ercolano *et al.*, 2016). Annual precipitation values range between 200 and 300 mm. The landscape corresponds to the Terraced Levels Unit (Rial, 2001), comprised of alluvial levels of sedimentary material forming extensive blankets that have gentle relief between elevations 138 and 170 masl. In the plains of the terraced levels, some depressions act as shallow lakes, mainly dependent on the snow load. The soils are about 30 cm thick and have a 10 cm A1 horizon of sandy loam texture with abundant organic matter. The remaining 20 cm are clayey and correspond to the B2 horizon, which rests on rocks (Rial, 2001).

In the terraced levels, there is a maar of approximately 1 km², a product of regional volcanism and canyons carved by runoff that dissect them (Rial, 2001). The largest canyon is the Mack Aike. Its headwaters are at 160 masl, and its confluence with the Gallegos River is at 66 masl. It has an approximate extension of 29 km and a wide valley (between 150 and 390 m) through which a permanent watercourse flows. Its bottom is between four and 13 meters below the level of the plains, providing shelter and an important supply of pastures. The frequent use of the canyon by guanacos means that they die here more frequently than in other areas, regardless of extreme winter stress events.

The southern part of the study area corresponds to the northern limit of the Pali Aike Volcanic Field. Here, the basaltic lava flows, and volcanoes offer shelters such as walls, rock shelters, and caves that, together with the erratic blocks, were used by hunter-gatherer populations (Bird, 1988; Barberena, 2008; Borrero & Charlin, 2010).

The typical plant community in the area is the dry grassy

steppe, dominated by the Fuegian coiron (Festuca gracillima), accompanied by grasses or small herbs such as Rytidosperma virescens and Carex andina. Additionally, shrubs like calafate (Berberis microphylla) and mata negra (Mulguraea tridens) are present (Prieto et al., 1999; Oliva et al., 2001; Oyarzabal et al., 2018). The main fauna includes guanacos, carnivores such as the puma (Puma concolor), the red fox (Lycalopex culpaeus), and the gray fox (Lycalopex griseus). Bird species

found in the area include the rhea (*Rhea pennata*), the caracara (*Caracara plancus*), and the black-chested buzzard-eagle (*Geranoaetus melanoleucus*) (Albrieu & Ferrari, 2000; Manero, 2000).

#### **MATERIALS AND METHODS**

The study presented here involved systematic field observations of two massive winter kills of guanacos that

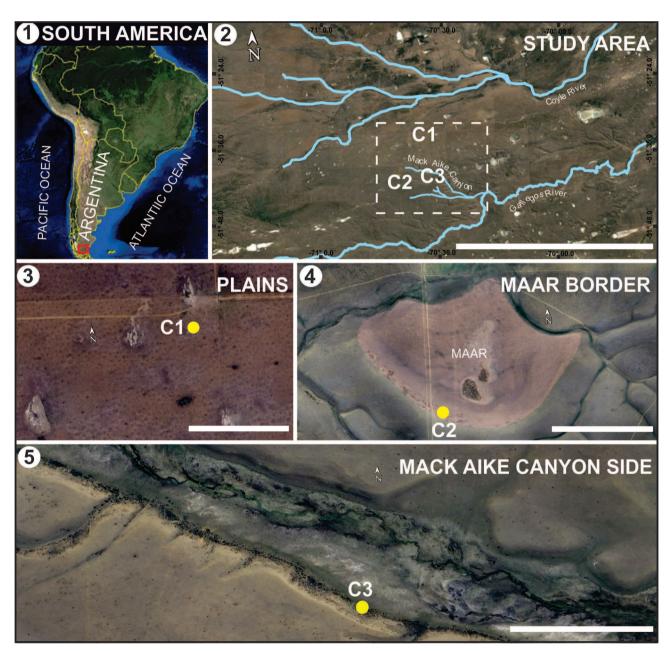


Figure 1. Study area where taphonomic observations are carried out; 1, Location of the study area in South America; 2, Detail of the study area and studied concentrations (Scale bar= 700m); 3, Detail of the location of Concentration 1 (Scale bar= 300m); 4, Detail of the location of Concentration 2; the orange shadow indicates the maar area (Scale bar= 700m); 5, Detail of the location of Concentration 3 (Scale bar= 450m).



occurred in 2020 and 2023 and were surveyed over five years (2021–2025) in the Coyle-Gallegos Rivers interfluve. Samples were collected from three distinct sectors: plains, maar border, and Mack Aike Canyon side (Figs. 1.3-5). Our observations were made during the austral summer, between February and March of each year. Information was collected using variable size transects depending on accessibility, visibility, and distribution of carcasses. All isolated individuals and concentrations were georeferenced. Sex, age, weathering stage (sensu Behrensmeyer, 1978), degree of disarticulation, and carnivore action were determined for each individual. Mortality profiles were constructed for the samples from the different sectors. A soil penetrometer was used to judge the feasibility of burial in each sector. Samples for genomic analysis were also collected in 2021 and 2022 (Leggieri et al., 2024).

In each sector, guanaco carcasses that appeared isolated or concentrated (two or more individuals) were counted and examined. Three concentrations, one in each sampled sector, were selected for longitudinal monitoring, or long-term follow-up of specific carcasses to register changes in different variables.

In this paper, we present and discuss in more detail the results of the monitoring of one of the plains concentrations (Concentration 1), where we were able to record different events of mass and individual deaths. Comparisons were made with concentrations from the other two sampled sectors: Concentration 2 (maar border) and Concentration 3 (Mack Aike canyon side), which vary significantly in their topography. This variation informed us, among other things, about the conditions for preserving skeletal remains, the potential fossil stability associated with burial, and the recognition of aggregation behaviors leading to mass deaths. We discuss the tempo of accumulations in Concentration 1, which refers to the duration of the process from the deposition of the carcasses to their complete recycling or burial of the bones. This information is evaluated in relation to potential cycles. For this purpose, among other concepts, the settling in effect is used, formulated on an experimental basis (Petraglia & Nash, 1987), with confirmations in several cases of systematic regional records (Bernáldez Sánchez, 2009). In the case of Concentration 1, settling in refers to the moment when, after the relatively accelerated changes undergone by the carcasses during the initial months after snow melting, decomposition, disarticulation, and displacement by carnivore activity and other processes seem to slow down, and the bones begin to stabilize as time goes by.

This is due to the elements reaching a state of equilibrium or stasis with the environment and local meteorology. Although it does not imply the interruption of processes, it basically refers to a marked decrease in horizontal displacements and vertical migration. In a way, this is related to the concept of retarding or decelerating factors of environmental dynamics; for example, the effect of snow or shrubs covering the bones. In our discussion, we will add other factors resulting from the particular dynamics of the accumulations produced by mass mortalities.

In our case study, the main formational forcing factors —understood as those agents and processes that make up the configuration of a fossil assemblage— are related to winter stress and generally involve accumulations of snow, cold, hunger, or their combination within a framework of shelter-seeking by the guanacos. The aggregation of carcasses in different years in the same places made it necessary to change the scales of the records. Over the years, longitudinal tracking of individual carcasses forming part of the concentrations, especially Concentration 1, became more complex, leading us to a coarser-grained assessment. While this might seem to be a problem, observations on longer scales, even if less precise, are useful insofar as they seek to reconstruct accumulation cycles over the long term. We also included deaths prior to our first observation of dead animals in 2020 to evaluate these long-term processes. This sample consists of 15 mandibles and other disarticulated elements displaying advanced weathering, which we believe correspond to individuals that were part of older winter kills. This inference is based on the presence of several 6-9-month-old guanacos (Fig. 2).

The search for cycles includes those dictated by the rhythms of the massive deaths and those dependent on the geomorphological characteristics of the death sites. These cycles involve factors that affect the exposure time of the carcasses and, therefore, their duration on the surface.

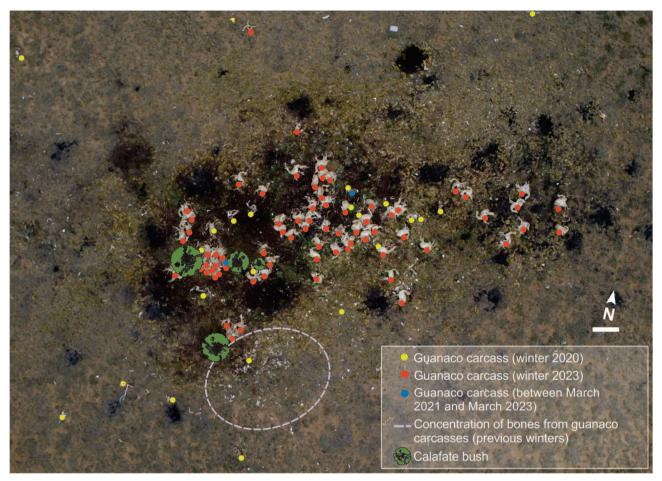


Figure 2. Distribution of dead guanacos around *calafates* during the winters of 2020, 2023, and pre-2020 in Concentration 1 (plains). Scale bar= 2m. Note the dung accumulation around and under the guanacos.

#### **RESULTS**

There were 945 guanaco carcasses assigned to winter stress deaths in the three sectors studied, distributed in the following events: winter 2020 (n= 482) and winter 2023 (n= 463) (Tab. 1). In general terms, the mortality profile of the total sample of winter 2020, analyzed in detail in Belardi *et al.* (2025), corresponds to selective deaths, with a significant number of first-year individuals. On the other hand, the profile of 2023 winter deaths resembles that of live populations with a significant number of prime individuals.

#### **Plains**

In this sector, large accumulations of carcasses are recorded, generally associated with the location of *calafate* bushes that are distributed in the form of patches. For example, in the death event of 2020, 19 concentrations

were recorded in this sector, five of which were composed of more than 20 individuals (Belardi *et al.*, 2025). On many occasions, the guanacos died in a lying position and huddled against each other (Fig. 3), a posture they adopt as a thermoregulatory mechanism that prevents heat loss by convection (de Lamo *et al.*, 1998; Lamuedra González, 2015). Over time, overlaps of carcasses associated with these locations were generated, configuring cases of generic redundancy, that is, depositions in the same space in general, without being specifically in the same *loci* (Hietala & Stevens, 1977).

In Concentration 1, 33 individuals corresponding to the deaths in the winter of 2020 were observed, most of them forming two groups, one around the *calafate* bushes and the other a few meters away from them (Fig. 4). We also observed the presence of a wide cover of dung of varying thickness (approximately 5 to 10 cm) as a result of the



TABLE 1 - Frequency of guanacos killed by winter stress in 2020 and 2023 recorded in different environments of the Coyle-Gallegos River interfluye.

Sector	2020	2023
Plains	255	334
Maar border	123	38
Mack Aike Canyon side	104	91
Total	482	463



Figure 3. Example of guanacos lying down, with their legs flexed and huddled against each other around *calafate* bushes in the plains sector.

defecation of, presumably, the individuals who took refuge in the area.

Longitudinal monitoring of these carcasses allowed us to record the disarticulation and displacement of anatomical portions due to the action of carnivores, birds of prey, and, possibly, trampling (Álvarez *et al.*, 2022; Belardi *et al.*, 2025). During our visits in 2022 and 2023, two new individuals were recorded and added to this concentration, and we cannot attribute them exclusively to winter stress. The

accumulation produced in 2023 in Concentration 1 as a consequence of a new event of winter stress was 69 carcasses, and again included individuals deposited around *calafate* bushes. This new death event created a mat of overlapping carcasses, with one from 2020 and others deposited in 2023 (Figs. 5.1–2). Other carcasses were also deposited at varying distances from the bushes (Fig. 2). This case of specific redundancy, or precise use of the same *locus* (Hietala & Stevens, 1977), is the main driver for the need to change



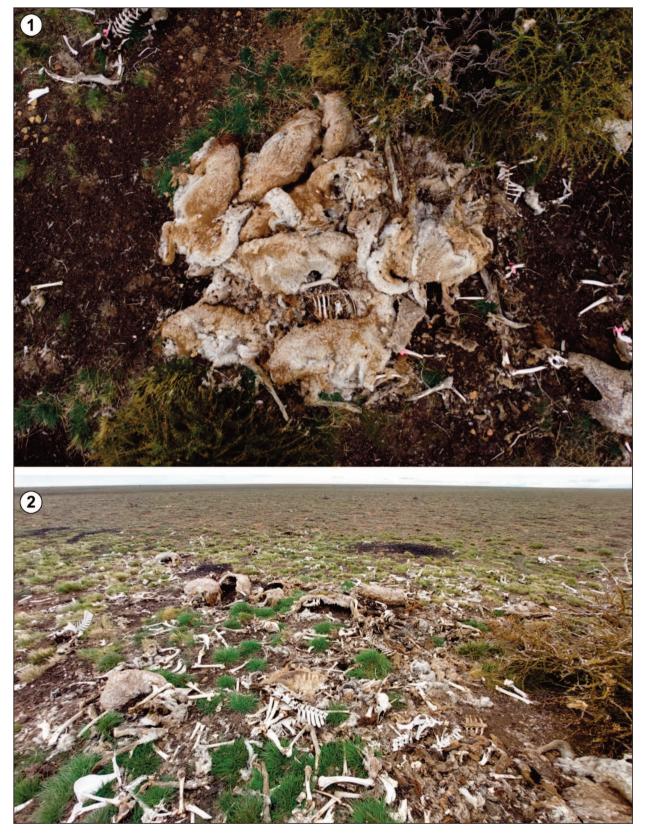
Figure 4. Drone image of Concentration 1 corresponding to winter 2020 deaths (photo taken in March 2022). Scale: the telescopic ruler seen in the image measures 2 m.

the scale of analysis in Concentration 1. Not only will the tracking of carcasses from the previous event —guanacos killed in 2020— be compromised after the last visit in 2025, but a stage begins in which, as a consequence of the progress of disarticulation and displacement of portions and bones, it will be increasingly difficult to recognize to which individual corresponds and consequently, to which death event each bone belongs. It is important to note that strict superimpositions, like those seen in Concentration 1, by adding fresh carcasses that begin their own accelerated period of disarticulation and decomposition, delay the processes underway on the previous carcasses deposited underneath, particularly the settling in effect. This delay is mainly the result of the overlapping carcasses limiting the access of carnivores to the carcasses deposited in 2020, which in turn, slows down the process of bone disarticulation. Our observations and surveys in the plains report that the possibility of vertical migration of bones is minimal, given the poor penetrability (requiring between 9 and 26 strikes for a penetration of 5 cm) of the soils (aridisols), which is detrimental to their long-term preservation. The only form of potential burial is in the accumulations of dung near the bushes. The long-term preservation of such surface accumulations is short, so they only function in the short term. Although we have detected spatial overlaps of some archaeological materials with modern carcass concentrations along the transect in the plains, the potential for confusion of these short-lived palimpsests is very low.

#### Maar border

In this sector, the distribution of the carcasses is a little more homogeneous than in the plains, mainly due to the





**Figure 5.** Examples of bone mats in the plains. **1,** 2020 and 2023 deaths in Concentration 1 (photo taken in March 2024); **2,** 2020 and 2023 deaths in another concentration with carcasses in the process of dispersal (photo taken in October 2024).

topography and the abundance of shrub vegetation (calafate and mata negra) that is more evenly distributed. In this location, we observed bone displacements not only due to the action of carnivores but also due to gravity acting in combination with surface water runoff. Longitudinal tracking of the 10 carcasses of the concentration monitored in this environment (Concentration 2), allowed us to detect displacements caused by the latter process (Fig. 6). The lack of sedimentation at the upper edge of the maar leads to low penetrability, requiring between 7 and 16 strikes for a penetration of 5 cm, while in the looser sediment of the talus 4 to 11 strikes are needed for the same mark. This situation, together with the slope of about 14°, creates favorable conditions for bone displacement. Some bones find their equilibrium point in topographic traps or bushes where the carcasses, articulated portions or individual bones are trapped, with good possibilities of burial due to the accumulation of fine sediment by wind and water action, or eventually reach the flat sector, where they may or may not be buried. Displacements occur, in many cases, along with gullies resulting from runoff. Recurrent passage of groups of guanacos and sheep (Ovis aries) trampling and kicking bones, aided by gravity, end up moving them towards the foot of the slope (Fig. 6). This process of reptation will produce a selective stabilization effect on the slope and at the foot of the slope. Over time, sedimentation and bioturbation (e.g., trampling) will lead to the burial of part of the skeletal elements in selected slope sectors, mainly at its foot. These varied conditions offer some alternatives for long-term preservation.

#### Mack Aike Canyon side

On the protected slope of the canyon, we observed less concentrated carcasses resulting from winter stress, also related to the presence of *calafate* and *mata negra* bushes. Longitudinal follow-up of the 10 guanaco carcasses from Concentration 3 showed that articulated portions and bones are displaced by the action of carnivores and gravity towards the canyon bottom, where better burial conditions exist due to wind and water sedimentation, pedogenesis, and trampling. Here, soil penetrability is high, with extensive areas where 4 to 6 strikes were needed for a penetration of 5 cm. The permanent presence of water on the canyon

bottom favors the growth of herbaceous vegetation (*mallines*), mainly composed of Cyperaceae, Juncaceae, and Poaceae (Peri *et al.*, 2024), leading to the development of soils with greater thickness (molisols) compared to other areas. These conditions favor long-term preservation, as evidenced by partially articulated and buried guanacos deposited since at least 4500 years BP (Belardi *et al.*, 2025).

In short, we found that burial possibilities are minimal in the plains (the primary focus of this study), moderate on the border of the maar, and higher in the Mack Aike Canyon side. Given the abundant and widely distributed archaeological record of the canyon, the high likelihood of burial may result in the formation of mixed assemblages of naturally deposited bones and artifacts (Belardi *et al.*, 2025).

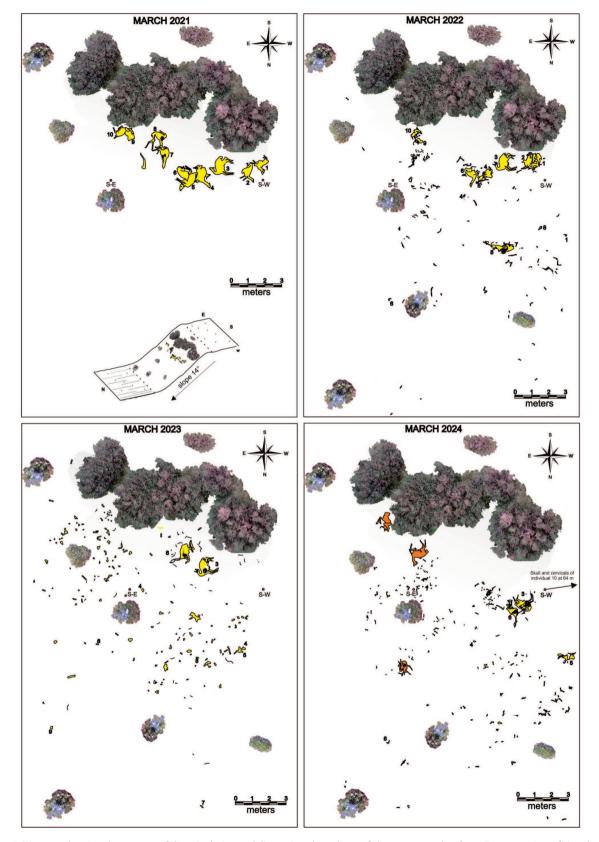
#### DISCUSSION

The following evaluates the main variables involved in the accumulation processes of guanaco carcasses along the three concentrations.

#### Regularity of the phenomenon

Discussion of mass bone accumulations in the fossil record has highlighted that "The long-term preservation and taphonomic signatures of a weather-related bone assemblage", including winter stress, depend on a variety of attributes that are difficult to predict (Rogers & Kidwell, 2007, p. 15), which is partly due to the limited research on these processes associating mass deaths with climate. A quick comparison with accumulations associated with water bodies or floods, which offer good burial and preservation conditions, suggests that instances of winter deaths with preservation potential are relatively rare (Rogers & Kidwell, 2007). However, in South America, we have good archaeological and paleontological examples of accumulations in aquatic environments, such as Paso Otero 1, Río Salado, or Ponsonby (Lepetz et al., 2003; Gutiérrez & Kaufmann, 2007; Tonni et al., 2008), but not of winter stress. Therefore, a fundamental question is whether these winter "climatic" deaths of animals constitute an unusual phenomenon. We think they are not. Not only have recent cases been recorded in Patagonia (Borrero, 1990, 2007; Estévez Escalera & Mameli, 2000; Rindel & Belardi, 2006; Vázquez, 2006; Belardi & Rindel, 2008), but also elsewhere in the world





**Figure 6.** Diagram showing the process of disarticulation and dispersion slope down of the carcasses that form Concentration 2 (Maar border). The yellow carcasses correspond to the winter 2020 deaths and the orange ones to those of 2023.

(Martinka, 1967; Berger, 1983, 1986; Schallery Junrang, 1988; Weigelt, 1989; Okarma et al., 1995; Scorolli et al., 2006; Warchałowski et al., 2015). In any case, the richness of bone accumulations in the Argentine Pampas has been highlighted (Weigelt, 1989), undoubtedly based on some important precedents, such as Darwin's observations on the coast of the Santa Cruz River. There, he observed concentrations of guanaco carcasses "in certain circumscribed spaces, which were generally bushy" ... "beneath and amongst the bushes" (Darwin, 1906, p. 159f.). These cases predate western cattle colonization, so they are not phenomena affected or caused by it. Darwin's observations show that the remains were abundant, showed no carnivore marks, and did not appear to have been transported. Later observations made in 1900-1901 near the mountain range (Prichard, 2003) confirm the phenomenon's importance and independence from livestock settlement. Similar observations were made even earlier by Bynoe on the shores of the Gallegos River (Darwin, 1906).

#### Causes

The causes of large winter climatic accumulations can be basically discussed in terms of the role of cold and hunger, both of which are associated with very cold winters, likely linked to previous summers with low productivity in pastures or significant droughts (Lamuedra González, 2015). These situations can be understood from animal physiology (Speth & Spielmann, 1983; Sturzenbaum & Borrelli, 2001; Belardi & Rindel, 2008). On the other hand, the parasitic load on animals in cold conditions, with low nutritional levels, is associated with massive mortality of guanacos in Cabo Dos Bahías, Chubut (Beldomenico *et al.*, 2003).

The starvation hypothesis proposes that when animals cannot migrate from the sectors most exposed to snow accumulation at the onset of snowfall, they starve. A paradigmatic case was presented by Johannes Weigelt (1989), who comments on the severe winters that affected wapiti (*Cervus canadensis*) in Jackson Hole (United States of America) at the beginning of the 20th century. Animals that could not migrate to the lowlands consumed hay, so they were hunted or moved to places without food. This case, although very old, is clearly affected by livestock expansion. But there are other cases not affected by human

activities, such as the mortality of bison (Bison bison) in Bighorn Basin (Wyoming, United States of America) in the winter of 1886-1887 (Frison, 2014) or others (Weigelt, 1989). In the Cabo Dos Bahías wildlife reserve, Chubut province, the mass death of 300 guanacos was recorded during the winter of 2000. The deaths were attributed to starvation following a severe drought that considerably limited the forage supply (Beldomenico et al., 2003). In the particular case of our study, during fieldwork, we observed that several guanacos had vegetation in the abdominal cavity in the process of digestion, which leads us to think that starvation could not have been the cause of death. However, this is more complex to evaluate. On the other hand, the hypothesis linking deaths to sudden drops in temperature (Weigelt, 1989) is supported by certain characteristics observed in the assemblages. In our study, abundant guanacos seeking refuge in well-defined areas such as the bushes indicate that the animals arrived before this sudden temperature drop. Still, we have records from other locations in southern Patagonia that clearly reflect this phenomenon. The position of many of the animals in the surveyed assemblages (lying down with flexed legs; Fig. 3) and their stacking suggest events of synchronous deaths among many of them. However, both situations can occur in the same event. These alternative winter stress scenarios do not require empty stomachs (animals in poor nutritional condition). Though the overall nutritional status of the animals is an important condition that significantly impacts the threshold temperatures tolerated and the likelihood of survival in the low temperatures of extreme winters. The causes of death related to cold or starvation may be part of the same process that we could call multicausal (Weigelt, 1989).

#### Locations

Our observations show concentrations of carcasses on slopes that offer greater shelter and around *calafate* and *mata negra* bushes, a situation already observed in other Patagonian regions such as Cabo Dos Bahías (Lamuedra González, 2015) and related to the search for refuge during storms and wind protection. The proximity of molle (*Schinus molle*) bushes or rocky shelters functioning as attractors of carcasses has also been observed (Belardi & Rindel, 2008).



In any case, in our study, the association with bushes is dominant, as it constitutes the most ubiquitous refuge.

In Concentration 1, accumulations of guanaco dung were identified, forming a trail that ended in the *calafate* bushes. This trail implies the use of established access routes to these refuges, likely created by the simultaneous arrival of groups of guanacos or by the use of relatively snow-free areas due to successive arrivals. The surroundings of the bushes that concentrate the carcasses are characterized by a relatively continuous layer of dung of variable thickness.

#### Spatial overlapping

A characteristic of the samples from the interfluve of the Coyle-Gallegos Rivers is the large number of overlaps of carcasses. The overlapping carcasses in different events and within the same event create large and relatively specific concentrations, including cases resembling a continuous mat of overlapping carcasses over previous concentrations. There are former modern records of animals stacked exactly one on top of the other at Lake Cardiel, at the Los Guanacos 3 rock shelter, where "Only minimal portions of certain bodies were able to be seen because they were almost completely covered by other individuals" (Belardi & Rindel, 2008, p. 47). The cases from the interfluve plains record concentrations of a greater number of individuals and differ from previous records in Tierra del Fuego (Estévez Escalera and Mameli, 2000; Vázquez, 2006; Borrero, 2007). Regarding the number of deaths, the overlap of individuals and their effects, the case of 193 feral horses (*Eguus caballus*) that died in a thunderstorm in the Tornquist Reserve, southwest of the Pampas region, is relevant. In the short span of two days between the event and the record, several groupings of carcasses were observed, some of which were partially trampled and buried in the mud (Scorolli et al., 2006). This demonstrates that even on the scale of a single event, records of individuals can not only be difficult to control but can also create vertical displacements with the potential for long-term preservation.

#### Putrefaction and disarticulation

Although we will not delve into the details of the successive disarticulation of carcasses and some retarding effects of this process, we do not want to overlook some observations. Mass die-offs, especially when they result in concentrated carcasses, slow down the disarticulation process (Burgett, 1990). Our case study, represented by carcass samples from the three sectors studied, is also comparable to that recorded by Todd (1987) for carcasses of cows (*Bos taurus*). This author describes that cows were stacked in a circular fashion seeking shelter in Plumbago Canyon (United States of America). Todd observed that the assemblage creates a "unique taphonomic microenvironment" (Todd, 1987, p. 109), in which carnivore action was concentrated at the edges (Todd, 1987) and uses it as an analog for studying bison from the Horner II site (Wyoming, United States of America).

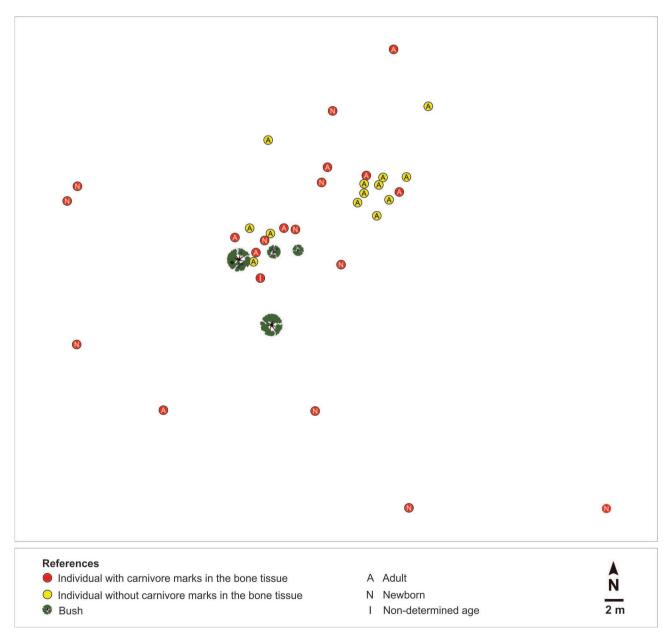
Our case study also presents a particular pattern, similar to the one described by this author. Figure 7 shows schematically the distribution of carcasses from the 2020 kill event in Concentration 1. There is a semicircular distribution of scattered carcasses showing tooth marks away from the sector with the highest concentration of guanacos, most probably displaced by carnivores from the original deposition *locus*. The type and size of the marks, in addition to the presence of scats and footprints, allowed us to consider foxes as the main carnivore acting upon carcasses. The count indicates that 20 of 33 individuals in this concentration show carnivore marks (61%). Another striking fact is that 11 of the 20 guanacos are younger than 12 months (55%), especially those located in the semicircle in Figure 7.

Todd also notes that "the proximity of carcasses" (Todd, 1987, p. 147) conditions disarticulation patterns and that the rotting process "often keep hide, particularly on the down ward surface, moist and enhance its potential for rapid decay and consumption by invertebrate scavengers", leading to early disarticulation "of the lower limbs through rapid deterioration of the surrounding hide ..." (Todd, 1987, p. 149; see also Bernáldez Sánchez, 2009, p. 49). Observations at Wind Cave National Park, United States of America, on carcasses of buffalo (Bubalus bubalis) and other large and mediumsized mammals (Burgett, 1990) also showed that the lack of intense predator activity generates conditions for the persistence of microfaunal activity, particularly during the warm season when carcasses are not frozen. By comparing the preservation of the different bone concentrations generated by the mass death of guanacos

at the Paso Otero 1 site (Necochea district, Pampas region), Gutiérrez (2006) proposes that the spatial distribution of bones in discrete accumulations generated a differential microenvironment, with unique preservation characteristics for each of them. These microenvironments provided protection to the bones, accelerating or retarding the rate and intensity with which certain agents and processes acted on them (Gutiérrez, 2006).

In Concentration 1, carnivore activity constitutes an

accelerating agent of disarticulation and dispersal. In our second visit to this concentration, *i.e.*, 20 months after the 2020 mass death event, although half of the carcasses preserved their anatomical integrity and death position, we observed that some individuals suffered further disarticulation and dispersal of anatomical portions (*e.g.*, hind and forelimbs). Some skeletal portions were displaced up to 80 m from the original death site (Belardi *et al.*, 2025).



**Figure 7.** Schematic distribution of carcasses of dead guanacos in 2020 in Concentration 1. The red circles correspond to individuals with carnivore marks in the bone tissue.



#### Mummification

Part of the stabilization process in the guanaco assemblages seems to involve, in certain cases, natural mummification, probably favored by the dryness and wind that characterize the study area. Todd (1987) observed cases of natural mummification of dead cows in the boreal autumn that "remained frozen in a bloat stage until the next April when night-time temperatures began to be consistently above freezing. By the time decay began in the spring, winds and sun had dried the // hide to a tough armor-like covering that has held the skeletons encased for at least 4 years" (Todd, 1987, pp. 109–110). It is, then, a two-phase process that reaches an equilibrium upon mummification and eventually a second equilibrium after the reinitiated process of fragmentation and disarticulation. A similar situation was recorded with massively dead cows in Sierra Baguales in 2008, as well as in isolated guanacos in the Magallanes steppe, Chile (L. A. Borrero, personal observation), and has been systematically recorded and studied in the Puna (Nasti, 1994-1995).

#### **Accumulation cycles**

The duration of an accumulation cycle depends on a variety of formational forcing, erosion, trampling, rainfall (Todd, 1987; Wang & Martin, 1993; Bernáldez Sánchez, 2009) and retarding factors such as shade, vegetation cover, snow or ice cover, mummification potential, and traps limiting sunlight access (Behrensmeyer, 1978; Todd, 1987; Sutcliffe, 1990; Wang & Martin, 1993). Only long-term work can narrow down the influence of these different factors for any given area.

A cycle can be completed by the disappearance of the bones, either by total recycling or the action of other processes such as burial or transport by different agents. The alternative to burial eventually involves fossilization. Significant cycles can also occur without the disappearance of all the bones, as occurs in the cases of mummification just mentioned. The key to determining the length of such cycles is the settling in effect. The time to stasis is the *tempo* corresponding to a given combination of substrates, climates, and contexts, culminating in a relatively static state of things for a significant time. In the case of Concentration 1, the averaged sample was recorded and evaluated in

several stages, cumulatively, in which different forms of stasis are recognized. We learnt that these processes may took several months, particularly when harsh winters occur, thus retarding the stabilization phase. The final destination of practically all the samples recorded in the plains will probably be complete recycling, so these cases of stasis just constitute temporary phases. The study of winter deaths from Cabo San Pablo, Tierra del Fuego, ended when the bones of the carcasses deposited 17 years earlier could no longer be identified on the surface (Borrero, 2007), which does not imply that complete recycling has occurred, since there is evidence of vertical migration and burial of bones. In turn, at least part of the carcasses under study were covered by a beaver dam. When the area was revisited in 2005, 2010, and 2011, the beaver dams appeared progressively abandoned, and no bones attributable to the original carcasses could be detected, although many were initially marked with metal plates.

An alternative to consider is that the bones on the surface are constantly renewed with carcasses resulting from new deaths. A continuous bone rain, which refers to bones deposited as a result of natural deaths, seems unlikely, as any depositional hiatus exceeding 20 years will have virtually no bones on the surface, since that is the time required for the complete recycling of guanaco skeletons. The lack of evidence of mass death during the harsh winter of 2024 indicates that there are no linear processes and that directions can change so that the renewal of carcasses by new deaths need not be eternal. The long-term cycles of use of places by animals can change under a number of circumstances, and areas that now receive a continuous bone rain may just cease to receive it because the animals stop frequenting the area. In any case, the continuation of observations in the long term still has the potential to surprise us since we are exploring uncharted territory. At the same time, as we shall see, the information already recorded has good informative potential on a comparative scale.

Our observations on the maar border and the Mack Aike Canyon side should also be mentioned. The first case reports accumulation cycles on slopes. These present variations in bone preservation mechanisms, depending on the possibility of burial in the upper part. If this is limited, there are numerous downslope depositional alternatives in topographic traps or bushes (see also Belardi & Rindel, 2008), so they are not merely continuous reptation avenues, a fallacy already recognized by Nash and Petraglia (1987). Their archaeological importance is well demonstrated (Martin & Borella, 1999; Ozán *et al.*, 2015).

On the slopes of the Mack Aike Canyon, we find the opposite case of the plains. The protection from severe climatic conditions (e.g., strong and icy winds) offered by the sides of the canyon attracts both human occupations and guanacos. This sector is a place where there are both opportunities for burial and possibilities for burial to be relatively definitive. In other words, conditions are suitable for long-term preservation. Taphonomic evidence is complemented, in these cases, by fossil evidence, which not only records guanacos that have died of natural causes since the middle Holocene but also shows the preservation of articulated parts (Belardi et al., 2025). Therefore, they allow us to evaluate to what extent the cases of sub-recent bones buried in articulated or disarticulated positions support previous studies on the "natural bone rain" that contaminates archaeological sites and also to recognize assemblages formed independently of human activity (Borrero, 1990; L'Heureux & Borrero, 2002). The cases of burials in the canyon are part of what we can see as contamination cycles, in which at least part of the stabilization process culminates in archaeological contexts.

#### CONCLUSIONS

The guiding question of this paper is what situations create spatial overlap of guanaco carcasses on the interannual scale, and what are the possibilities for bone preservation? Plains show the most repeated massive spatial overlap, but, at the same time, provide few burial opportunities, limited to short-term burial conditions that depend on dung accumulations. These conditions generally lead to total recycling. The stability cases observed, for example, due to spatial overlapping, are not definitive, as there are no conditions for open-air preservation. Temporary decoupling caused by specific overlays of carcasses and other retarding factors prolong these surface exposure cycles for a short time. We mention the alternative of deposition of new carcasses, in shorter time frames than

those granted by complete recycling. These potential cycles are summarized in a tension between weathering and the regularity of mass die-offs. But we also saw that even burial does not appear to be definitive in this area. These are assemblages that will inevitably continue to rearrange, transform, and recycle.

What are the characteristics of the averaged samples recorded? First of all, sedimentation in the plains is so low that it is difficult for them to enter the fossil record and contaminate eventual archaeological records. In any case, it would be very unlikely that eventual burial, if it occurs, would be cumulative or even definitive. Burial-exposure cycles are undoubtedly an essential part of the formation dynamics of the plains.

An important observation is that this negative evidence about the short duration of palimpsests-or even elements of them-in the plains is informative, particularly for archaeological finds at high altitudes related to obtaining lithic raw materials or other extractive tasks. In many of these cases, bones are not preserved due to low sedimentation, but activities related to the exploitation of faunal resources cannot be excluded. They should also serve to discuss models of human circulation in mountainous areas (Dawe & Kornfeld, 2017) or Martin's (1973) invisibility argument.

Time and sedimentation rate are crucial in applying most mixing criteria. The latter variable seems to covary positively with the carcasses' articulation and the elements' bone integrity. We have proposed what appears to be a paradox. The large mass die-off event of the plains may remain hidden in the long term, while a contemporary one in the canyon with a lower frequency of die-offs may leave a detectable stratigraphic signal. What we know of other cases of mass die-offs also show the difficulties in detecting mass die-off in the Fuego-Patagonian area, since an event that seems much more visible, such as the San Pablo event where bone burial was demonstrated (Tierra del Fuego; Borrero, 1990, 2007), will hardly be recognizable as massive in the stratigraphic record given the scarce spatial overlap of cases.

The study of guanaco deaths due to winter stress from an actualistic perspective has allowed us to discuss the dynamics of fossil record formation processes and the



implications for the regional archaeology of Patagonia. Moreover, the unexpected taphonomic recurrence of death events in the same spaces opened new questions. It forced us to rethink our research, especially our contribution to the study of cycles and time averaging of bone accumulations.

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#### REFERENCES

- Albrieu, C. & Ferrari, S. (2000). La estepa. In *El Gran Libro de la Provincia de Santa Cruz* (pp. 280–301). Milenio Ediciones y Alfa Centro Literario.
- Álvarez, M. C., Gutiérrez, M. A., Massigoge, A., Borrero, L. A., Kaufmann, C. A., Recofsky, M., & Belardi, J. B. (2022). Acumulaciones de Restos Óseos en Nidos de Carancho (*Caracara plancus*, Aves, Falconiformes) de la Patagonia Austral. Implicaciones Tafonómicas y Arqueológicas. *Revista del Museo de Antropología*, *15*(3), 219–234. http://doi.org/10.31048/1852.4826.v15.n3.37850
- Barberena, R. (2008). Arqueología y Biogeografía Humana en Patagonia Meridional. Sociedad Argentina de Antropología.
- Behrensmeyer, A. K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology*, *4*,150–162.
- Behrensmeyer, A. K. & Hook, R. W. (1992). Paleoenvironmental Contexts and Taphonomic Modes. In A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H-D. Sues, & S. L. Wing (Eds.), Terrestrial Ecosystems through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals (pp. 15–136). The University of Chicago Press.
- Belardi, J. B. & Rindel, D. (2008). Taphonomic and archaeological aspects of massive mortality processes in guanaco (*Lama guanicoe*) caused by winter stress in Southern Patagonia. *Quaternary International, 180*, 38–51. https://doi.org/10.1016/j.quaint.2007.08.021
- Belardi, J. B., Carballo Marina, F., & Campan, P. (2022). Distribuciones de artefactos líticos, cronología y el modelo de pisoteo (Borrero 1988): los médanos de la costa norte del lago Viedma (Santa Cruz, Patagonia argentina). *Chungara. Revista de Antropología Chilena*, 54, 521–534.
- Belardi, J. B., Borrero, L.A., Carballo Marina, F., Kaufmann, C. A., Massigoge, A., Álvarez, M. C., & Gutiérrez, M. A. (2025). Modern guanacos (*Lama guanicoe*) killed by winter stress in Southern Patagonia (Argentina). Taphonomic and Archaeological Implications. In G. Wong & A. Klemmer (Eds.), *Zooarchaeology: Beyond Human Subsistence* (pp. 1–60). University of Utah Press.
- Beldomenico, P. M., Uhart, M., Bono, M. F., Marull, C., Baldi, R., & Peralta, J. L. (2003). Internal parasites of free-ranging guanacos

- from Patagonia. Veterinary Parasitology, 118, 71-77.
- Berger, J. (1983). Ecology and Catastrophic Mortality in Wild Horses: Implications for Interpreting Fossil Assemblages. *Science*, 220, 1403–1404.
- Berger, J. (1986). Wild Horses of the Great Basin: Social Competition and Population Size. University of Chicago Press.
- Bernáldez Sánchez, E. (2009). Bioestratinomía de macromamíferos terrestres de Doñana. Inferencias ecológicas en los yacimientos arqueológicos del S.O. de Andalucía. BAR International Series 1978.
- Bird, J. B. (1988). *Travels and Archaeology in South Chile*. University of Iowa Press.
- Bonfili, J. O. (2024) Olas de frío en Río Gallegos. Informe técnico inédito. Unidad Académica Río Gallegos, Universidad Nacional de la Patagonia Austral, Río Gallegos. MS.
- Borrero, L. A. (1988). Estudios tafonómicos en Tierra del Fuego: su relevancia para entender procesos de formación del registro arqueológico. In H. D. Yacobaccio (Ed.), *Arqueología Actualidad y Perspectivas* (pp. 13–32). Ediciones Búsqueda.
- Borrero, L. A. (1990). Taphonomy of guanaco bones in Tierra del Fuego. *Quaternary Research*, *34*, 361–371.
- Borrero, L. A. (2007). Longitudinal Taphonomic Studies in Tierra del Fuego, Argentina. In M. A. Gutiérrez, L. Miotti, G. Barrientos, G. Mengoni Goñalons, & M. Salemme (Eds.), *Taphonomy and Zooarchaeology in Argentina* (pp. 219–233). BAR International Series 1601, Archaeopress.
- Borrero, L. A. & Charlin, J. (2010). Arqueología del Campo Volcánico Pali Aike, Argentina. In L. A. Borrero & J. Charlin (Eds.), Arqueología de Pali Aike y Cabo Vírgenes (Santa Cruz, Argentina) (pp. 9–30), CONICET-IMHICIHU.
- Burgett, G. R. (1990). The Bones of the Beast: Resolving questions of faunal assemblage formation processes through actualistic research. [Unpublished PhD Thesis]. Department of Anthropology, University of New Mexico.
- Darwin, C. (1906). Journal of Researches into the Geology & Natural History of the Various Countries Visited During the Voyage of the Beagle Round the World, under the Command of Capt. Fitz Roy. Dent & Sons.
- Dawe, R. J. & Kornfeld, M. (2017). Nunataks and Valley Glaciers: Over the Mountains and through the Ice. *Quaternary International*, 444, 56–71. https://doi.org/10.1016/j.quaint.2017.03.062
- de Lamo, D. A., Sanborn, A. F., Carrasco, C. D., & Scott, D. J. (1998). Daily activity and behavioral thermoregulation of the guanaco (*Lama guanicoe*) in winter. *Canadian Journal of Zoology*, 76, 1388– 1393. https://doi.org/10.1139/z98-070
- Ercolano, B., Coronato, A., Tiberi, P., Corbella, H., & Marderwald, G. (2016). Glacial geomorphology of the tableland east of the Andes between the Coyle and Gallegos River valleys, Patagonia, Argentina. *Journal of Maps 12*, 304–307. https://doi.org/10.1080/17445647.2016.1206840
- Estévez Escalera, J. & Mameli, L. (2000). Muerte en el canal: experiencias bioestratinómicas controladas sobre la acción sustractora de cánidos. *Archaeofauna*, *9*, 7–16. https://doi.org/10.15366/archaeofauna2000.9.001
- Frison, G. C. (2014). Rancher Archaeologist. A Career in Two Different Worlds. The University of Utah Press.
- Gifford-Gonzalez, D. (2018). An Introduction to Zooarchaeology. Springer.
- Gutiérrez, M. A. (2006). Efectos, agentes y procesos tafonómicos en el área Interserrana bonaerense. *Relaciones de la Sociedad Argentina de Antropología*, 31, 201–228.

- Gutiérrez, M. A. & Kaufmann, C. A. (2007). Methodological criteria for the identification of formation processes in guanaco (*Lama guanicoe*) bone assemblages in fluvial-lacustrine environments. *Journal of Taphonomy*, *5*, 151–176.
- Hietala, H. J. & Stevens, D. S. (1977). Spatial analysis: multiple procedures in pattern recognition. *American Antiquity*, 42, 539–559.
- Lamuedra González, L. D. (2015). Variables ambientales asociadas a la distribución espacial de guanacos muertos (*Lama guanicoe*) en la Reserva Provincial Cabo Dos Bahías, Chubut, Argentina. [Unpublished BA thesis]. Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco.
- Leggieri, L. R., Anello, M., Peralta, D., Túnez, J. I., Di Rocco, F., Poljak, S., Flores, C., Alunni, D., Belardi, J. B., Gutiérrez, M. A, Álvarez, M. C., Massigoge, A., Kaufmann, C. A., Borrero, L. A., Borghi, C., Demartini, J., Petracci, P., Sotelo, M., Marbán, L., Kathiravan, P., Rudolf, P., Marín, J. C., Cárcamo, J. G., & Carmanchahi, P. (2024). Delineating genomic features for wild guanaco conservation. *Biological Journal of the Linnean Society, 143*, blae087. https://doi.org/10.1093/biolinnean/blae087
- Lepetz, S., Lefèvre, C. & Pellé, E. (2003) Los guanacos de la turbera: nota sobre un depósito natural. *Magallania*, *31*, 415–418.
- L'Heureux, G. L. & Borrero, L. A. (2002). Pautas para el reconocimiento de conjuntos óseos antrópicos y no antrópicos de guanaco en Patagonia. *Intersecciones en Antropología*, *3*, 29–40.
- Manero, A. (2000). Los mamíferos de Santa Cruz. In *El Gran Libro de la Provincia de Santa Cruz, Tomo 1*, (pp. 311–319). Milenio Ediciones y Alfa Centro Literario.
- Martin, P. S. (1973). The discovery of America. *Science*, *179*, 969–974. https://doi.org/10.1126/science.179.4077.969
- Martin, F. M. & Borella, F. (1999). Tafonomía de Tierra del Fuego: reevaluación de la arqueología de Cabeza de León. In J. B. Belardi, P. M. Fernández, R. A. Goñi, A. G. Guráieb, & M. De Nigris (Eds.), Soplando en el viento... Actas de las III Jornadas de Arqueología de la Patagonia (pp. 439–450). Instituto Nacional de Antropología y Pensamiento Latinoamericano - Universidad Nacional del Comahue.
- Martinka, C. (1967). Mortality of northern Montana pronghorns in a severe winter. *Journal of Wildlife Management, 31,* 159–164.
- Massigoge, A., Rafuse, D. J., Álvarez, M. C., González, M. E., Gutiérrez, M. A., Kaufmann, C. A., & Scheifler, N. A. (2015). Beached penguins on the Atlantic Coast in the Pampas region of Argentina: Taphonomic analysis and implications for the archaeological record. *Palaeogeography, Palaeoclimatology, Palaeoecology, 436*, 85–95. https://doi.org/10.1016/j.palaeo.2015.06.045
- Müller, P. L. S. (1776). Erste Classe, Säugende Thiere. *Des Ritters Carl von Linné vollständiges Naturalsystem nach der zwölften Lateinischen Ausgabe.*
- Nasti, A. (1994–1995). Desarticulación natural y supervivencia de partes anatómicas: tafonomía de vertebrados modernos en medioambientes puneños. *Palimpsesto. Revista de Arqueología*, 4, 70–89.
- Nash, D. T. & Petraglia, M. D. (1987). Natural Formation Processes and the Archaeological Record: Present Problems and Future Requisites. In D. T Nash & M. D. Petraglia (Eds.), *Natural Formation Processes and the Archaeological Record* (pp. 186–204). BAR International Series 352. Archaeopress.
- Okarma, H., Jędrzejewska, B., Jędrzejewski, W., Krasiński, Z. A., & Miłkowski, L. (1995). The roles of predation, snow cover, acorn crop, and man-related factor of ungulate mortality in Białowieża Primeval Forest, Poland. *Acta Theriologica*, 40, 197–217.
- Oliva, G., González, L., Rial, P., & Livraghi, E. (2001). Áreas ecológicas

- de Santa Cruz y Tierra del Fuego. In P. Borrelli & G. Oliva (Eds.), Ganadería ovina sustentable en la Patagonia austral. Tecnología de Manejo Extensivo (pp. 41–82). Ediciones Instituto Nacional de Tecnología Agropecuaria.
- Oyarzabal, M., Clavijo, J., Oakley, L., Biganzoli, F., Tognetti, P., Barberis, I., Maturo, H. M., Aragón, R., Campanello, P. I., Prado, D., Oesterheld, M., & León, R. J. C. (2018). Unidades de vegetación de la Argentina. *Ecología Austral*, *28*, 40–63. https://doi.org/10.25260/EA.18.28.1.0.399
- Ozán, I. L., Borrero, L. A., Borrazzo, K., & L´Heureux, G. L. (2015). Tafonomía en pendientes: El caso de cerro Sin Nombre (Tierra del Fuego, Argentina). In J. Rubin de Rubin & C. Favier Dubois (Eds.), *Geograpueologia na América do Sul* (pp. 285–330). Universida de Pontificia.
- Peri, P. L.; Gaitán, J., Díaz, B., Almonacid, L., Morales, C., Ferrer, F., Lasagno, R., Rodríguez-Souilla, J., & Martínez Pastur, G. (2024). Vegetation Type Mapping in Southern Patagonia and Its Relationship with Ecosystem Services, Soil Carbon Stock, and Biodiversity. Sustainability, 16(5), 2025. https://doi.org/10.3390/su16052025
- Petraglia, M. D. & Nash, D. T. (1987). The impact of Fluvial Processes on Experimental Sites. In D. T. Nash & M. D. Petraglia (Eds.), *Natural Formation Processes and the Archaeological Record* (pp. 108–130). BAR International Series 352. Archaeopress.
- Prichard, H. (2003). En el corazón de Patagonia. Zagier & Urruty Publications.
- Prieto, A., Stutz, S. & Pastorino, S. (1999). Arqueopalinología de la Cueva Las Buitreras (Provincia de Santa Cruz, Argentina). *Praehistoria*, 3, 169–181.
- Rial, P. (2001). Grandes unidades de paisaje. In P. Borrelli & G. Oliva (Eds.), Ganadería ovina sustentable en la Patagonia austral. Tecnología de Manejo Extensivo (pp. 22–40). Ediciones Instituto Nacional de Tecnología Agropecuaria.
- Rindel, D. & Belardi, J. B. (2006). Mortandad catastrófica de guanacos por estrés invernal y sus implicaciones arqueológicas: el sitio Alero Los Guanacos 1, lago Cardiel (Provincia de Santa Cruz, Argentina). Magallania, 34, 139–155. http://dx.doi.org/ 10.4067/S0718-22442006000100009
- Rogers, R. R. & Kidwell, S. M. (2007). A Conceptual Framework for the Genesis and Analysis of Vertebrate Skeletal Concentrations. In R. R. Rogers, D. A. Eberth, & A. Fiorillo (Eds.), *Bonebeds: Genesis, Analysis, and Paleobiological Significance* (pp. 1–62). The University of Chicago Press.
- Schaller, G. & Junrang, R. (1988). Effects of a snowstorm on Tibetan Antelope. *Journal of Mammalogy, 69*, 631–634. https://doi.org/10.2307/1381361
- Scorolli, A. L., López Cazorla, A. C., & Tejera, L. A. (2006). Unusual Mass Mortality of Feral Horses during a Violent Rainstorm in Parque Provincial Tornquist, Argentina. *Mastozoología Neotropical*, 13, 255–258.
- Speth, J. D. & Spielmann, K. A. (1983). Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *Journal of Anthropological Archaeology*, 2, 1–31. https://doi.org/ 10.1016/0278-4165(83)90006-5
- Sturzenbaum, P. & Borrelli, P. (2001). Manejo de riesgos climáticos. In P. Borrelli & G. Oliva (Eds.), Ganadería Ovina Sustentable en la Patagonia Austral. Tecnologías de Manejo Extensivo. INTA-Santa Cruz (pp. 255–270). Ediciones Instituto Nacional de Tecnología Agropecuaria.
- Sutcliffe, A. J. (1990). Rates of Decay of Mammalian Remains in the Permafrost of Canadian High Arctic. In C. R. Harington (Ed.), Canada's Missing Dimension: Science and History in the Canadian



Arctic Islands, v. 1 (pp. 161–186). Canadian Museum of Nature.

Todd, L. C. (1987). Taphonomy of the Horner II Bone Bed. In G. C.

Frison & L. C. Todd (Eds.), *The Horner II Site: The Type Site of the Cody Cultural Complex* (pp. 107–198). Academic Press.

Tonni, E. P., Bonini, R. A., Molinari, A. E., Pomi, L. H., Prevosti, F. J., Carbonari, J. E., & Huarte, R. (2008). Análisis radiocarbónico en una tafocenosis de la región pampeana (provincia de Buenos Aires, Argentina): su vinculación con la Gran Seca de 1827–1832. Intersecciones en Antropología, 9, 307–311.

Vázquez, M., 2006. Tafonomía de la muerte y parámetros poblacionales. Guanacos en las bahías Valentín y Cambaceres, costa sur de Tierra del Fuego. In A. G. Austral & M. Tamagnini (Comp.), *Problemáticas de la Arqueología Contemporánea* (pp. 239–241). Universidad Nacional de Río Cuarto.

Wang, X. & Martin, L. (1993). Natural Trap Cave. *National Geographic Research & Exploration*, *9*, 422–435. https://doi.org/10.1016/j.quaint.2023.01.007

Warchałowski, M., Nowakowski, P., & Dancewicz, A. (2015). Effect of winter conditions on wild ungulates mortality in the Owl Mountains (Poland). *Folia Forestalia Polonica, series A, 57*, 187–193. https://doi.org/10.1515/ffp-2015-0018

Weigelt, J. (1989). Recent Vertebrate Carcasses and Their Paleobiological Implications. The University of Chicago Press.

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