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Behavioural biology of South American domestic camelids: An overview from a welfare perspective☆

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ABSTRACT

South American domestic camelids (SADC) have played a key role in the culture, economy, food security and livelihoods of ancient and contemporary societies in Andean countries. This is especially due to the capacity of alpacas and llamas to produce fibre and meat under extreme geographic and climatic conditions. In addition, the breeding and use of SADC as fibre, meat, pet and sheep herding animals has become popular in Europe, North America and Oceania. However, research and scientific literature concerning the behaviour and welfare of both species is scarce, dispersed, and with little visibility compared to other species. Therefore, the objective of this literature review is to compile the international scientific literature on the most relevant aspects of the behaviour of llamas and alpacas, especially in terms of practical aspects which could be used to improve their welfare in the many production systems in which they are raised.

1. Introduction

South American camelids have been used by human Andean groups since the first settlements more than 11,000 years ago, and have contributed strategically to the dispersion of the first American hunters in the Andes, who benefited from their meat, skin, fur, and even their bones for the manufacture of tools (Vilá and Arzamendia, 2020). These camelid species include the wild guanaco and vicuna, as well as the domestic llama and alpaca (Wheeler et al., 1995a, b). Currently, although alpaca and llama breeding has spread rapidly in recent decades in North America, Australia, New Zealand and Europe (Neubert et al., 2021), the Andean countries maintain the world's largest South American domestic camelid (SADC) population with more than 3.8 million llamas and 4 million alpacas (Smith-Davila et al., 2019). The Andean country with the largest inventory is Peru with 90% of the world's alpacas and 32% of the world's llamas, while Bolivia has 64% of the world's llamas and 9% of the world's alpacas (Mamani-Linares et al., 2014). Eighty per cent of the alpacas and almost all of the llamas in both countries are in the hands of small producers with mixed herds composed of llamas, alpacas, sheep, and cattle, basically constituted in peasant communities, the remaining 20% of alpacas are bred on medium-sized farms and socially owned enterprises (Casaverde and Huanca, 1985; Pizzaro et al., 2019).

The breeding of these species plays a crucial role in the livelihoods of high Andean farming communities, where the llama is considered a multi-producer animal, valued for its meat, fibre, manure and transport (Szpak et al., 2014; Gandarillas et al., 2016). Alpaca breeding has been mainly oriented towards the production of fibre and, more recently, meat, to supply the gastronomic boom in Peruvian cuisine (Miranda-de la Lama et al., 2022). This is especially due to a specialised international market that demands high quality fibre and an incipient interest of the gourmet market, that is interested in nutritional properties of their meat (Miranda-de la Lama et al., 2022). In addition, SADC production is growing in the original Andean communities where they are a valuable local resource that attracts foreign exchange from the export of fibre and animals of high genetic quality (Wurzinger and Gutiérrez, 2022). It is therefore to be expected that production systems for these two species will become increasingly intensive and that consequently animal welfare problems will become more evident, as has been the case for other livestock species (Miranda-de la Lama et al., 2022). This becomes even more relevant if we take into account the growing social concern for welfare in South America, which is stimulating changes in the stakeholders along the agri-food chain in the region (Estévez-Moreno et al., 2022). In addition, alpacas and llamas are considered charismatic

☆ Dedicated to the memory of our beloved fathers, Mario Villarroel and Wilfredo Miranda.

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species that bring out empathetic feelings and concerns for their welfare among consumers and citizens in general (O'Shaughnessy, 2008).

Nevertheless, the scientific and technical literature on the behaviour and welfare of SADCs is scarce and scattered, and the research generated in Andean countries has little international visibility because it is usually restricted to academic or technical reports (Miranda-de la Lama et al., 2022). This paper presents a descriptive review of general aspects of the domestication, biology, sense organs, communication and behaviour of llamas and alpacas. Two types of information sources were used; a) desk research based on theses, research reports and grey literature generated especially in the Andean area, and b) scientific literature searches focused on digital databases (Google Scholar, ScienceDirect, Scopus, Scielo and Redalyc) published in English, Spanish and Portuguese. The search was delimited by the combination of the terms "llamas, alpacas and South American camelids" finding 210 papers or scientific reports, of which only 136 papers presented direct evidence related to the behaviour and/or welfare of SADC, and were included in our review. Thus, the aim of this paper is to review current knowledge on the behaviour and welfare of alpacas and llamas in livestock production systems, using an integrative approach.

2. Domestication and history

Mitochondrial genetic analyses confirm that llamas were domesticated from the guanaco subspecies (*L.g. cacsilensis* and *L.g. guanicoe*) and alpacas from vicuna, as well as interbreeding among llama and alpaca (Varas et al., 2020). The llama is the larger of the two domesticated SADC measuring between 100 and 120 cm at the withers, with a weight between 100 and 250 kg, while the alpaca measures only 80–90 cm at the withers and weighs between 55 and 90 kg (Björklund, 2014). Unlike other domestic Artiodactyls, such as goats, sheep, and pigs, SADC have a larger body mass than their wild ancestors (Goñalons, 2008). In the case of alpacas, it has been postulated that hybridisation with the larger guanaco has had a strong effect on their overall size through the cumulative effect of the two parental genomes (Balcarcel- et al., 2021). In contrast, the much less hybridised llama has a body size more similar to that of the guanaco (Kadwell et al. 2001).

During the course of SADC domestication, a number of environmental and cultural changes took place in the Andean region between 3200 and 4500 m above sea level (Yacobaccio and Vilá, 2016). Archaeozoological evidence identifies the domestication hot-spot of the alpaca in the humid plateau ecosystems of the central Andes (now Peru) 6000–7000 years ago, and that of the llama in the dry southern plateaux of what are now Peru, Chile and Argentina (Goñalons, 2008; Scanes, 2018). Llamas were bred especially for the transport of goods and fibre production, while alpaca were selected for fine fibre production (Fan et al., 2020). As early as 3000 years ago alpaca and llama fibre were used to manufacture textiles, as evidenced by archaeological findings in the Atacama Desert. During the Incan rule, the products of state-controlled textile production comprised the currency of the empire (Azémard et al., 2021). Furthermore, SADC provided other valuable products such as meat, skin, bones, and dung, as well as religious offerings (Mader et al., 2018). In the indigenous Quechua language, *Allpaka* is related to *allpa*, which means "land", and *kamay*, which means "to animate". Thus, *allpa-kamasqa* can be loosely translated to "animals of the living land" (Vilá and Arzamendia, 2020). *Llama* (singular) or *llamakuna* (plural) is also a primitive or underived Quechua word, and does not have a meaning distinct from the animal it represents (Guamán, 2018).

In the last twenty years, several studies of pre-Hispanic camelid mummies have demonstrated the existence of alpaca and llama breeds that have no current counterparts in the Andes region (Azémard et al., 2021). This has revealed a greater diversity of forms during the pre-Hispanic era that was later reduced, as one of the consequences of the Spanish conquest (Goñalons, 2008). Within a century of the Spanish conquest of Cuzco in 1532, administrative and taxation records document the precipitous decline and virtual disappearance of previously extensive herds throughout the Andes (Wheeler et al., 1995a, b It is estimated that up to 80–90% of all llamas and alpacas disappeared during this short period (Varas et al., 2020) together with approximately 80% of the human population, leading to the economic and social disintegration of native society (Wheeler et al., 1995a, b). The drastic reduction of alpaca and llama populations may have been the result of: (a) a measure to control local human populations by destabilizing their livelihoods, (b) ignorance of the superior quality of their fibre for the textile industry, and (c) interest in the introduction and establishment of cattle, goats and sheep as a means of territorial control (Gade, 2013). Simultaneously, inbreeding and hybridization increased as herd management and breeding practices were abandoned, resulting in lower fibre quality and less consistent colour patterns in alpacas and less consistent phenotypes in llamas (Barreta et al., 2003). Hybridization between llamas and alpacas has been demonstrated in a recent whole genome sequencing study. Fan et al. (2020), reported that up to 36% of the modern alpaca genome probably derives from hybridization with llamas. Modern alpacas and llamas are the outcome of an extensive hybridization that has been attributed to the species near demise following the Spanish conquest, a hybridization that apparently did not affect guanacos and vicuñas (Diaz-Maroto et al., 2021).

Unfortunately, unlike many other domestic farm animals, there is no written history associated with the llama and alpaca (Varas et al., 2020). According to Kadwell et al. (2001), orally transmitted knowledge about both species was largely lost during the Spanish conquest, and breeds or ecotypes disappeared as both human and native domestic livestock populations declined. Currently, two varieties of alpacas are recognized, one known as the Huacaya, with a short and crimped fleece, and the other called Suri, which has longer and wavy fibres that are considered the finest. In demographic terms of the worldwide alpaca population, there is a predominance of the Huacaya type, from which 90% of alpaca fleece is processed (Barreta et al., 2012). For llamas, there are two varities, the Chaku, which is woolly, and the Kara, which is short-fibered and specialized for carrying loads (Antonini, 2010).

3. Biology

Camelids originated in North America during the Middle Eocene (ca. 45 Ma) and remained restricted to that continent for most of the Cenozoic, before spreading to Eurasia and probably Africa during the latest Miocene (6 Ma), and to South America during the Early Pleistocene (1.8 Ma). The modern tribes of camelids, the *lamines* and *camelines*, radiated during the Early to Middle Miocene and became extinct in North America at the end of the Pleistocene, but survived in South America and the Asia-Africa, respectively (Bravo-Cuevas et al., 2012). Currently, the family *Camelidae* has three genera designated as *Camelus*, *Vicugna* and *Lama* (Stanley et al., 1994). The first genus is known as the Old-World camelids because they come from the arid plains of Africa and Asia, while the remaining two genera are from the highlands of South America, known as New-World camelids. The genus *Camelus* includes two domestic species, the Arabian camel (*Camelus dromedarius*, one hump) and the Bactrian camel (*Camelus bactrianus*, two humps), as well as the wild camel (*Camelus ferus*, two humps). The Vicugna genus includes a wild species which is the vicuna (*Vicugna vicugna*), and a domestic species which is the alpaca (*Vicugna pacos*). The Lama genus has a wild species which is the guanaco (*Lama guanicoe*), and a domestic one known as the llama (*Lama glama*) (Vásquez et al., 2020). In general, members of the *Camelidae* family are herbivores and pseudo-ruminants because they have only three stomach compartments, analogous to the rumen, omasum and abomasum (Hund and Wittek, 2018). Camelids differ from other artiodactyls by having nail-covered plantar pads on the feet instead of hooves, and thus belong to the suborder Tylopoda (Fowler, 2011). The nail or claw is small and weightless. Because of this anatomical feature, they preserve the soil against compaction and can easily traverse dangerously steep slopes (Sumar, 1988). All *Camelidae* species have 37 pairs of chromosomes, and both Old-World camelids and New-World camelids can interbreed within their genera, their offspring being fertile (Bravo et al., 2000).

New-World camelids are morphologically similar with inter-specific differences in fleece colour and size and have adapted to the diverse climatic conditions of the Andean region, ranging from the extreme aridity of sea level deserts to moist tundra and the pampa grasslands with differences in specific latitudinal and vertical distribution (Azémard et al., 2021) (Fig. 1). The fine, thick fleece is an important protection against the heat of intense solar radiation at high altitudes and in a treeless environment, as well as a means of thermal insulation from the sub-zero temperatures prevalent in the high Andean regions (Sumar, 1988). Currently, wild guanacos have a broad geographic distribution across a variety of open habitats (arid, semiarid, hilly, mountain, steppe) and temperate forest environments (Yacobaccio, 2021). The guanaco is the most widely distributed wild South American camelid in the region, being found in north-western Peru, in western and southern Bolivia, north-western Paraguay, and throughout the Andes of Chile and Argentina, where its distribution extends eastward to the Atlantic coast, and southward to the islands of Tierra del Fuego and Navarino. It is estimated that more than 90% of the total guanaco population is found in Argentina, mainly in the Patagonian region (Travaini et al., 2015). Meanwhile, wild vicunas live only in high-land environments above 3400 m in Peru, Bolivia, Argentina, and Chile. They are adapted to open grasslands and steppes. Although they prefer to graze in the humid wetlands or marshes, due to the presence of livestock in these wetlands, vicunas are usually found in the steppes (Yacobaccio, 2021). In the case of the alpaca, it is currently distributed in the Lake Titicaca basin, and in the Andean highlands of northern Chile and central Peru, and coastal sites in northern and southern Peru. Compared to the alpaca, the llama has a wider geographical distribution and presence in other ecosystems, as it is found in Colombia, Ecuador, Peru, Bolivia, northern and central Chile and north-western Argentina and its neighbouring areas (McLean and Niehaus, 2022).

Under the conditions of the Andean plateau (high altitude, variability and scarcity of forage quality and supply, high UV radiation), SADC are adapted to a seasonal semi-arid climate (Vélez-Marroquín et al., 2022). Thus, during the dry season (May to November), camelids are forced to forage on large amounts of fibrous (seasonally highly lignified) plants with many structural carbohydrates in the cell walls of the plants that are difficult to digest. During the wet season (December to April), camelids have access to tall grass, forbs and leafy vegetation (San Martin and Bryant, 1989). This seasonality forces animals to store fat deposits during the wet season that they can mobilize during the lean times of the dry season, when vegetation is scarce and of low nutritional quality (Fowler, 2011). In addition, water resources are very scarce in the semi-arid Andean climate, so SADC are extremely good at reabsorbing water from their spiral colon. More than 25% of the water entering the colon is absorbed before defecation (compared to 10% in cattle) and pelleted faeces already begin to form in the spiral colon (Vater and Maierl, 2018). To thrive at the high altitudes of the Andean plateau, alpacas and llamas show physiological adaptations as high haemoglobin oxygen affinity, small elliptical red cells with high haemoglobin concentration, a small increase in blood haemoglobin concentration, high muscle myoglobin concentration, more efficient O_2 extraction at the tissue and high lactate dehydrogenase activity (Llanos et al., 2007).

4. Sensory systems

In order to better understand the behaviour of SADC, we briefly review some of the particularities regarding their perception through sensory organs. Alpacas and llamas have large, prominent eyes with long eyelashes located on the sides of the skull, which provide excellent peripheral vision (>330°). However, their binocular vision, formed by the overlapping of the visual fields of the two eyes, is poor (Fowler, 2011). Both llamas and alpacas are dichromatic, that is, they only see shades of blue, yellow and grey (Gionfriddo, 2010). Vision in llamas appears to be different from that of alpacas. Willis et al. (2000) found that llamas are slightly myopic (nearsighted) and have some astigmatism (abnormal corneal shape), while alpacas are almost emmetropic (normal vision), although female llamas appear to be slightly more myopic than males. The reason for these differences is unknown, but may be related to differences in ocular size, especially axial length and corneal curvature (Metzler, 2020). Unlike old world camelids, the pupils of SADC eyes are horizontally oblong, like most artiodactyls (Harman et al., 2001). It has been postulated that the horizontal pupil function is an adaptation to aid surveillance against predators in the open field, so that the animal does not require excessive eye and head movements that could mistakenly alert the herd or reveal its position to the predator (Wang et al., 2015). Visual communications in SADCs is based on a series of postures and positions of the body, neck, tail and ears that allow them to communicate over long distances. In general, postures and neck postures are important for intergroup communication between adult males during advertising and territory defence, while ear and tail positions are especially used in conflict between group members (Aba et al., 2010). Schaffer et al. (2020) found that unlike guanacos, llamas have the ability to use the gaze of their conspecifics and even humans to obtain information about the environment such as location of food, predators and social interactions. However, in wild guanacos, it has been reported that groups use cooperative vigilance as the main antipredator mechanism by alerting each other through alert posture (animal standing with head and neck erect, ears erect pointing directly at stimulus or threat) and vocalisations (Taraborelli et al., 2012).

For gregarious species living in open habitats such as alpacas and llamas, visual displays are much more developed, although vocal communication can play a significant role in the exchange of information between conspecifics to promote successful adaptations to their habitat and social environment, to help them avoid danger, and to enhance reproductive success (Blank, 2021). Although SADC are only slightly vocal, alpacas are generally more vocal than llamas. Their most common vocalisations have been described as a humming (bleating), which is thought to be related to communication between group members. Other variations in intonation are described as a "separation hum" or a "distress hum", screams indicating extreme fear, and alarm calls expressed by high-pitched sounds described as "whistles" or "whinnies" (Fowler, 2008). The hearing of alpacas is similar to other artiodactyls (auditory range 40–32.8 kHz with a well-defined point of best sensitivity at 8 kHz), having good sensitivity to sound, even at low frequencies, but their sensitivity is not unique. At the most sensitive point, they hear better than pigs and horses, but not as well as cattle, goats and sheep. However, this difference is less than 10 dB (Heffner et al., 2014). The relatively poor localization acuity in alpacas and llamas is related to morphological and size alterations in the mesotympanic zone of the skull, attributable to a general reduction of cranial capacity as an indirect effect of domestication (Wheeler et al., 1995a, b). On another note, congenital deafness is a common defect in domestic South American camelids that present the blue-eyed white or BEW phenotype, which is white hair coat and solid blue eye colour, as opposed to white animals which have pigmented eyes (Anello et al., 2022). In a study by Gauly et al. (2005), it was found that about 80% of BEW llamas and alpacas were deaf. This anomaly should be considered during handling to identify vulnerable animals. At the farm level, the hearing ability of SADC can be assessed by observing their reactions to their environment when unrestrained (Whitehead and Bedenice, 2009).

Olfactory communication and signalling in SADC are especially supported by metatarsal and interdigital glandular tissue secretions. Although there are also large sebaceous glands in the ventral region of the tail and in the anal region, no function other than regional lubrication has been demonstrated (Chamut et al., 2016). The metatarsal patches are oval and alopecic, located on the medial and lateral surface of that region and have multilobulated holocrine glands. Their excretions signal alarm or permit individual identification via pheromones,

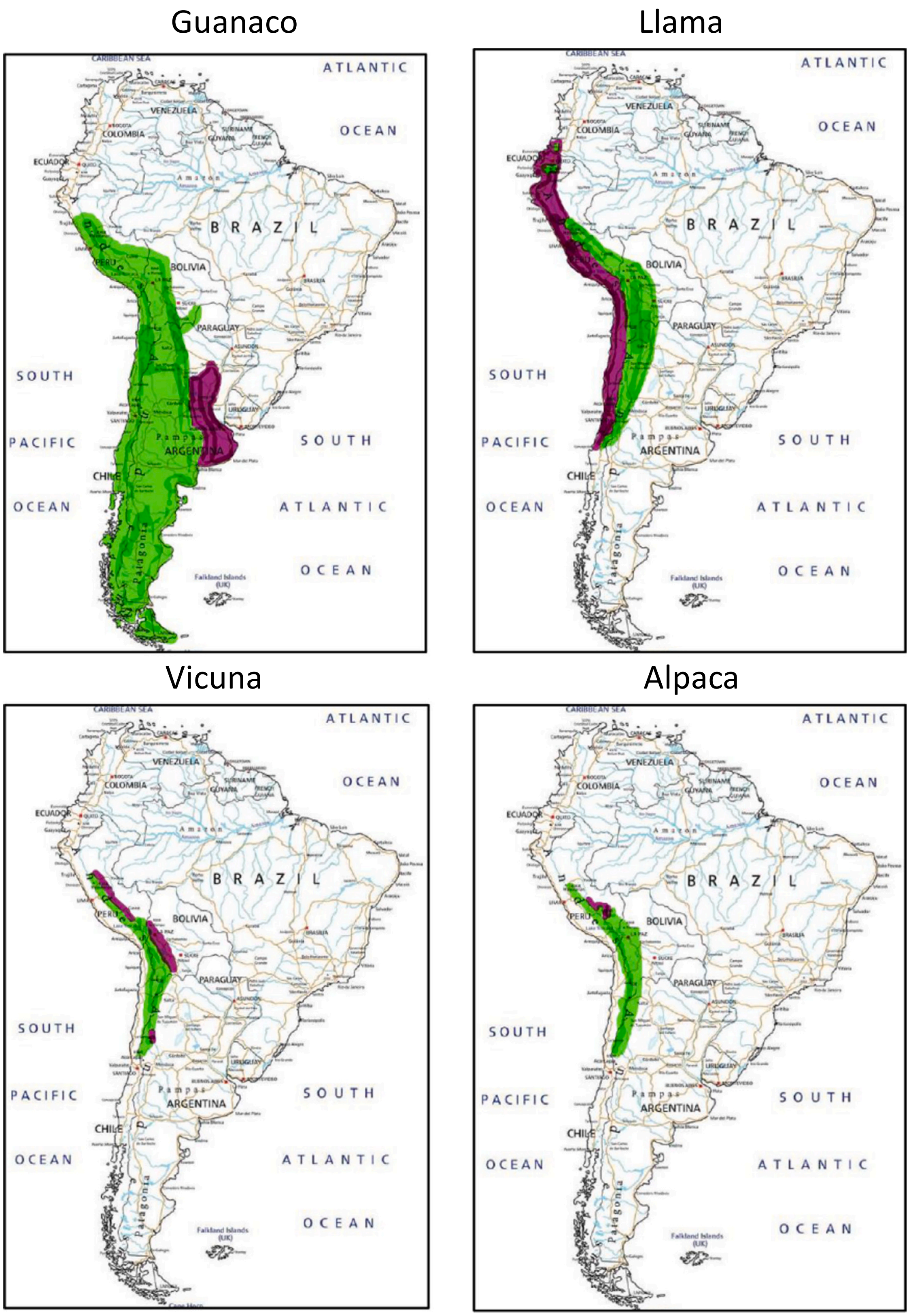

Fig. 1. Distribution of populations of llamas, guanacos, alpacas and vicuñas in South America. The areas shaded in green indicate the current distribution, while those shaded in purple indicate the pre-Hispanic original distribution, both shaded areas indicate the original distribution for each of the four species. In the case of llamas and alpacas, their current distribution is due to the fact that they are still part of the way of life of Andean communities because they have not been displaced by other domestic species (i.e. sheep and cattle) or other economic activities (i.e. tourism, agriculture, industry or migrations to the city).
Modified from McLean and Niehaus (2022).

perceived as "burnt popcorn" odour by humans (Fowler, 2011). While the interdigital glands are circumscribed eccrine tubular glands found on all four legs, their secretions are related to the secretion of sex pheromones (Chamut et al., 2016). Flehmen behaviour often occurs after sniffing the female's perineal region, fresh female urine or faeces (Lichtenwalner et al., 1998). The animal, usually a male, raises its head with a raised upper lip without curving it, and a slightly open mouth to capture and decode the odour message (pheromones) in the vomer-nasal organ (Tibary and Vaughan, 2006). Males, upon detecting a female in oestrus, exhibit this behaviour after smelling her urine (Aba et al., 2010). Flehmen also may be displayed by pregnant or females in oestrus when smelling the dung pile or the perineal area of another female (Bravo, 2014).

Pain differs from the classical senses because it is both a discriminative sensation and a behavioural impulse (painful experiences and behaviours), being important to maintain homeostasis (Craig, 2003). SADC, as prey animals, tend to show reduced sensitivity to painful stimuli (analgesic response) when exposed to predators or predation-related situations (Kats and Dill, 1998). This would explain some of the difficulties that handlers or veterinarians have to easily detect pain in llamas and alpacas, since they can be perceived as potential predators by the animals (Plummer and Schleining, 2013). However, like other animal species, SADC experience pain following noxious stimuli that can come about due to a range of conditions, from trauma and disease to production management procedures (Smith et al., 2021). The most obvious signs of pain in SADC include tachycardia, bruxism and tachypnoea, while signs of mild to moderate pain are anorexia, lethargy, excessive resting time, avoidance of contact and abnormal posture (Duncanson, 2012). More severe pain may result in recognisable pain manifestations, including violent movements such as rolling and twisting (Grubb, 2014). Aversive situations combining non-severe painful tissue injuries, fear of predation and corresponding palliative medical care can lead to capture myopathy in camelids (Biasutti and Dart, 2019). This myopathy is characterised by decreased blood flow of oxygen and nutrients to tissues, which increases lactic acid production, leading to extensive necrosis of skeletal muscle tissue. In addition, myoglobin released from dead muscle cells can cause fatal renal failure (Carmanchahi et al., 2011).

5. Maintenance behaviour

The activities involved in maintenance can be divided into several primary generic systems which are innate in origin and which during the animal's life are often modified in frequency and intensity by experience, physiological and health status (Fig. 2). The frequency of these activities and their distribution throughout the day can be used as indicators of animal welfare (Waiblinger et al., 2004). In alpacas reared in high mountain conditions, Rios et al. (1984) reported that their activities were distributed between grazing (78%), walking (7%), rumination-rest (4%) and drinking, dust bathing and defecation (11%). In the same study, it was observed that the calves followed the activity patterns of their mothers, except for the time spent ruminating, which was less.

Feeding involves a complex series of decisions and depends upon an elaborate array of mental, motor and digestive abilities (Quispe et al., 2021). Free ranging SADC need to find the right sort of habitat and then to find areas or patches of food before they can start looking for particular food items (Broom and Fraser, 2015). During pre-Hispanic times, domestic llamas were confined to the Andean regions of Peru, Bolivia, Chile and Argentina, especially in high altitude native grasslands called *pajonales*. Alpacas had a more restricted habitat in the high, humid highlands of Peru, Bolivia and northern Chile known as *bofedales*. *Pajonales* are extensive plant communities formed by a high stratum (between 0.5 and 1 m) dominated by perennial plants and very tall perennial and very lignified grasses, such as *Jarava ichu* and *Festuca dolichophylla*, in addition to a more diverse lower stratum (Castellaro et al., 2004). The *bofedales* are located in high humid mountain ecosystems and in dry ones occupying less surface area than the *pajonales*.

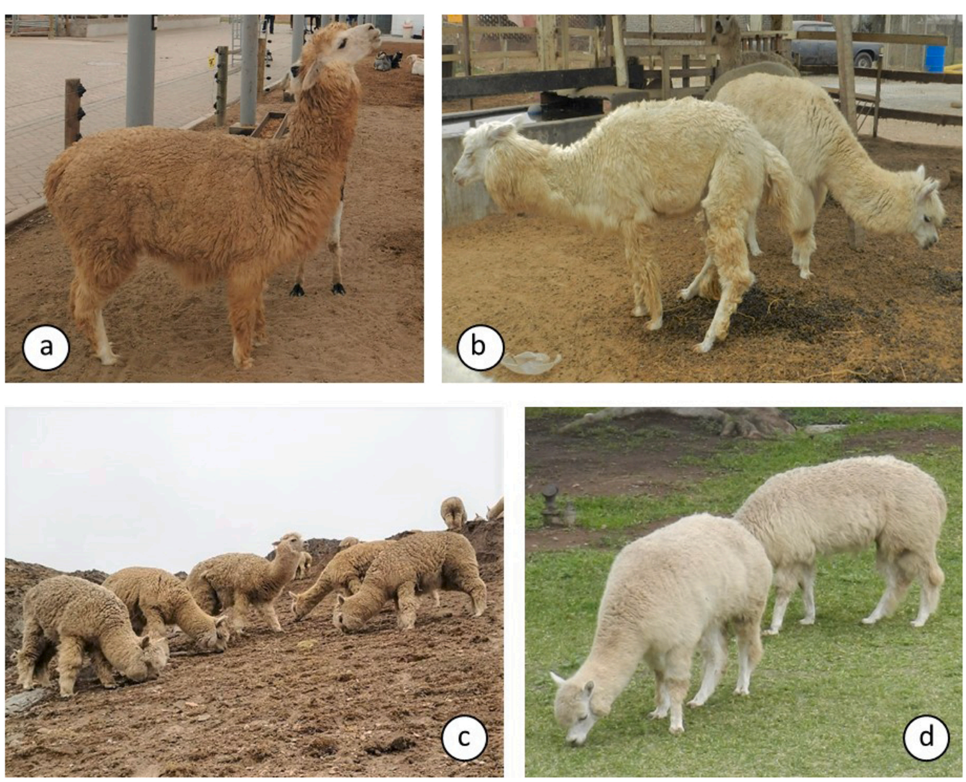

Fig. 2. Huacaya alpacas performing maintenance behaviours related to sensory communication a) Flehmen; b) use of latrines in pens; c) high altitude grazing and d) valley grazing.

Bofedales are formed by grasses, sedges and other herbaceous plants capable of forming dense emergent cushions above the flood level, with very slow growth (Reiner and Bryant, 1986).

SADC are adapted to very low-quality diets because they feed on herbaceous stratum and are considered mixed feeders (between grazing and browsing), according to vegetation availability in high altitude environments (Aba et al., 2010). However, alpacas prefer grasses, followed by sedges and reeds, while llamas have a strong preference for large quantities of coarse bunchgrasses and also browse on available shrubs and trees. Similar to alpacas, llamas consume very few forbs but select diets with mostly tall grasses, while alpacas select both tall and short grasses (Erdoğan et al., 2016). This selectivity is possible since camelids have a narrow snout and a prehensile upper lip, divided or with a cleft below the nose. Each half is highly discriminating and functions independently of the other (Cebra, 2014). The upper lip is used as a tactile sensory organ in food discrimination (Fowler, 2010). A wrap around stripping mechanism characterizes their grazing and browsing behaviour, and they are able to nip forage by virtue of a toothless upper fibrous raphe (Esteban and Thompson, 1988). Additionally, both species do not use their tongue to manipulate food, and it rarely protrudes from their mouth, making them unlikely to use salt licks (San Martín and Van Saun, 2013). The dental formula of each side in permanent teeth for llamas and alpacas (hypsodont dentition) is 1/3 incisors, 1/1 canines, 2/1 pre-molars and 3/3 molars (Gunsser, 2019). The upper incisor migrated caudally in the jaw and became the caniniform or fighting tooth. These look like upper canines and are usually removed in males to facilitate handling and assure safety (Esteban and Thompson, 1988).

Regarding water ingesting, according to Enke et al. (2022), llamas have a low frequency of water consumption, which indicates their adaptation to water scarcity, and they also have a tolerance to saline water for drinking, similar to that observed in goats. These same authors showed that llamas have a great sense of taste, normally tasting different sources of water before consuming larger quantities, while maintaining their diurnal rhythm of water intake. Alpacas and llamas suck water with their mouths slightly open to drink and have a strong preference for open water surfaces such as ponds, although they adapt well to float-valve drinkers that keep the water at a constant level. However, they are reluctant to drink polluted water and/or use push-valve water bowls where it is necessary to press a lever to obtain the water (Gerken et al., 2019).

In autochthonous grazing systems, SADC adjust to seasonal cycles where the abundance and quality of food varies dramatically over time, and periods of starvation are common (Wang et al., 2006). Therefore, llamas and alpacas may experience fluctuation in body weight and body condition due to the seasonal cycle of feast or famine (Bravo and Fowler, 2008). When using scores to assess body condition in SADCs, it is important to note the season of the year (wet or dry) when the assessment is made, as it will influence the body condition of the animals (Riek et al., 2019). This resistance to starvation is an adaptive capacity of both species to survive harsh Andean conditions, especially during the dry season when the availability of pasture and water are limited (Van Saun, 2006). This adaptive feature must be considered when breeding in non-native countries because animals can be overfed (Fowler, 2008). In fact, obesity has been documented as a major disease in SADC outside of South America (Fowler, 2011). Different body scoring systems exist for alpacas and llamas using scales of 1–5 and 1–10 (both from emaciated to obese) that include visual and tactile examination of the lumbar spine, withers, shoulders, ribs, legs, or pelvis (Hilton et al., 1998; Johnson, 1994). Currently, the most commonly used body condition score (BCS) is a scale of 1–5 (1 = emaciated; 2 = lean; 3 = optimal; 4 = overweight; 5 = obese). According to Wagener et al. (2021), an optimal BCS (3) would be characterised by a straight line between the dorsal spinous processes and the transverse processes of the lumbar spine, while a more concave line would be interpreted as a lower BCS, and a more convex line as a higher BCS.

Supplementation with high fibre concentrates prior to parturition, during parturition, mating and gestation has a positive effect on the reproductive performance of traditionally bred alpacas (Rojas et al., 2021). At the farm level, SADC do not have unique nutrient requirements and can be maintained on a diet of good quality grass hay or a mixture of grass hay and legumes (D'Alterio et al., 2006). Supplemental feeding of concentrates is usually not necessary, except for young growing stock, working animals and lactating females (Bravo and Fowler, 2008). Concentrate may be used for training (positive reinforcement), but overfeeding should be avoided (Bravo, 2015). Alpacas, when faced with changes in the type or presentation of food with which they are unfamiliar, abruptly reduce their consumption for a longer period of time than sheep and llamas, before recovering their normal level of consumption (Provenza and Balph, 1987). Therefore, pre-weaning training is a good strategy to reduce food neophobia and promote acceptance of novel foods. Castro-Bedriñana et al. (2017), found that the sensitive age of alpaca *cria* for early food learning is at three months of age, when they can be exposed to concentrate for more than 11 days for the food to be gradually considered part of the daily diet.

SADC use latrines for defecation and urination, and these can be visually identified as piles of dung accumulated in spatially confined areas in a lodge or pasture (Fowler, 2011). When approaching a latrine, the animal sniffs the pile, then kneads it with its front legs, and, if satisfied, turns around and adopts a squatting position, with the hind legs apart and forward under the body (Chamut et al., 2016). In intensive systems, camelids maintain the behaviour of defecating in latrines. Defecation usually comes first, followed immediately by urination. A healthy camelid usually visits the latrine two to four times a day. Frequent or prolonged visits, straining posture and frequent attempts to expel urine or faeces out of the pile are abnormal (Cebra, 2014). The presence of latrines plays an important role for intragroup orientation, helping to keep members of a family group together within their territorial boundaries. In addition, it is essential for intergroup communication between dominant males as part of their process of signalling territory and deterring potential contenders (Aba et al., 2010). However, in the wild some latrines are shared by vicunas or guanacos and llamas or alpacas (Chamut et al., 2016). According to Sumar (1988), the use of latrines has two consequences. The first related to their fertilizing effects that are especially noticeable downhill of the dung heaps at the beginning of the summer rainy season. The second is related to parasite control, since defecating only in the latrines interrupts parasite cycles. Other maintenance behaviours of interest related to the welfare of SADCs are those related to body care. In both species there is a marked tendency to scratch against hard surfaces such as posts, timbers and walls, and to wallow in dusty areas known as dust baths, which are large circular depressions in the ground where grass does not grow due to the camelids' repeated rolling (Matthews et al., 2020). SADC appear to use scratch and rolling sites to maintain the insulating properties of their fibre and to eliminate parasites (Aba et al., 2010). However, communal use of these substrates is also a source of external parasites transmission in the flock (Van Hoy et al., 2022).

6. Social and sexual behaviour

The social group is an essential component of the complex and dynamic environment of the individual, in which many strategies have evolved to improve survival and maintain group viability (Miranda-de la Lama et al., 2010). Social behaviour in South American camelids facilitates ecological integration of the group, improved protection against predators (i.e. pumas and Andean foxes), efficient foraging, easier potential access to sexual partners and group care of offspring (Bonacic, 2011). Despite domestication, the social behaviour of llamas and alpacas appears to be similar to that observed in guanacos and vicunas, respectively (Aba et al., 2010). The social organisation of SADC family groups is based on resource defence polygyny, defined as a territorial system in which males compete for access to food resources that are attractive to females. Thus, the number of females that a male retains to form a family group is correlated with the quantity and quality of resources in his territory (Panebianco et al., 2021). Within the family group there is a linear social hierarchy, with the adult male dominating the females and the adult females dominating the offspring (Aba et al., 2010). However, Correa et al. (2013), in a study with a captive group of guanacos found no evidence of hierarchical structure in the offspring, although contrary to other studies, females were more dominant than males. Furthermore, this authors also found that the establishment of dominance was not dependent on age, weight or offspring, and suggest the possibility that complex social dynamics are what allow animals to establish their hierarchical position within the group ontogenetically.

In the wild, a camelid population in a defined area is usually divided into the following three social groups: 1) a family group consisting of an adult male with a variable number of females and their offspring, 2) a group of single males with a variable number of individuals, including juveniles and adults, and 3) lone males who may be looking for females with which to form a new family group or very old males who were rejected by other groups (Aba et al., 2010). In these populations, males fight violently with each other to maintain territorial and family group control, with the dominant male spending most of his time patrolling and protecting the group (Wilson, 1982). Because of this behavioural attribute, llamas and alpacas have been used to guard herds of sheep and goats to protect them from potential predators (Duncanson, 2012). In Australia, castrated male alpacas are usually joined to a flock of sheep at a ratio of one alpaca per 100 sheep. No more than three alpacas should be used for a single herd as they tend to flock together rather than with the livestock they are guarding (Matthews et al., 2020). SADC have a marked aversion to dogs, even chasing and attacking them, so the use of dogs for camelid herding is not recommended (Sumar, 1988).

Pollard and Littlejohn (1995) found that when an individual alpaca was separated from a stable group, it experienced an increase in heart rate and performed specific behaviours, such as movement around the pen, vertical or horizontal head movements at the wall and door of the pen, nosing of the pen, and resting in ventral recumbence, as well as decreased appetite. However, these responses disappeared when the animal was restrained by the handler after being isolated from the group. If an animal is isolated for any clinical or handling procedure, it is recommended they always have visual or tactile contact with herd mates throughout the handling process (Vélez-Marroquín et al., 2022). Additionally, as in other livestock species, special care should be taken with the social mixing of animals of different origins in the same pen (especially males) as this will increase the frequency of aggression and injury (Smith-Davila et al., 2019). Spitting is part of the body language of llamas and alpacas and is used to express displeasure, establish the social order of the herd, and respond to threats (Gegner and Sharp, 2012).

Under Andean conditions, the mating season occurs from late November to April when weather is warm and humid during the "rainy season" (San-Martin et al., 1968). Under these conditions the offspring are born heavier due to the increased opportunity for the mother to feed on green forage during gestation (Smith et al., 1994). Alpacas and llamas are sexually monomorphic, showing sexual dimorphism only in the canine teeth, with the males having large teeth for fighting (Franklin and Johnson, 1994). Unlike goats, ewes and cows, SADC females have induced ovulation (Montelli et al., 2020). Most SADC females are sexually receptive at 12 months of age, although ovarian activity begins at 10 months. There is a relationship between body weight at the time of mating and subsequent natality, so it is recommended that females should weigh more than 33 kg (Sumar, 1996). Males have a fibroelastic penis and sigmoid flexure like ruminants (Duncanson, 2012), and show sexual interest at 1 year of age, although at that age only 8% of males lose penis-preputial attachment and can achieve intromission (El Zawam et al., 2020). This adhesion tends to gradually disappear over the course of sexual maturation under the influence of testosterone, whereby loss of preputial adhesions is achieved in 70% of males by two years of age and 100% by three years of age, when the male is reproductively mature and viable (Sumar, 1991). The pre-ovulatory LH surge and ovulation is driven by a protein present in the seminal plasma, and not by coital stimulation during mating (Silva et al., 2020; Carrasco et al., 2021). However, it is estimated that 5% of animals can ovulate spontaneously with only olfactory, auditory or visual stimuli (Fernandez-Baca et al., 1970). During the calving season and without the presence of males, females can remain sexually receptive for periods of up to 36 days, with a brief anoestrus of no more than 48 h (Pollard et al., 1995). The continuous association of males and females has an inhibitory effect on the sexual activity of males, and can even lead to the complete disappearance of their libido; however, they recover their sexual activity immediately after being introduced to a new herd of females (Mamani-Mondragón, 2014). On the contrary, when males and females are kept separately and are brought together at any time (e.g. once a month), both are sexually active all year round and females may give birth in different months (San-Martin et al., 1968; Fernández-Baca et al., 1970; Mamani-Mondragón, 2014).

Courtship in SADC is highly stereotyped and initiates when males trot after females at random (San-Martin et al., 1968). Aggressive behaviour toward other males has been observed, culminating in a direct confrontation with biting, neck wrestling and chest ramming that can lead to serious injuries, especially if the canine teeth are well developed (Tibary and Vaughan, 2006). Females may reject males when pregnant or under the influence of progesterone, and flee, kick or spit at the male (Fowler, 2008). Conversely, if the female (nulliparous or multiparous) accepts the male, she adopts a sternal decubitus position with her pelvis elevated to facilitate mating by the male, who places his metatarsals laterally to the female's sides and his feet flat on the ground in a "sitting" position (Pollard et al., 1994). Copulation by one or more pairs produces an auditory effect on other females in oestrus, who then approach to sniff the male and adopt the sternal decubitus position for the duration of the copulation of the observed pair (San-Martin et al., 1968). In this position, she may be mounted by other females who make pelvic movements similar to those of the male, however, such mounting is not sufficient to produce ovulation (Fernández-Baca et al., 1970).

Copulation is a prolonged event, averaging 19 min in llamas and 17 min in alpacas, with a range of 5–40 min (Bravo et al., 2002). During copulation, the male constantly emits an insufflating vocalisation known as "orgling", accompanied by dilation of the nostrils and tail movements, while the female remains still. Bravo (1994), has suggested that this vocalisation is a trigger to facilitate the neural response in the hypothalamus of the female for the stimulation of gonadotropin releasing hormone (GnRH). Pregnancy cannot be easily seen, even in the advanced stage in SADC, although mammary development can be observed one week before parturition with some enlargement of all four teats (Duncanson, 2012). A practical method to diagnose pregnancy is the introduction of males (vasectomised or whole) to the female herd 15 days after copulation. Non-pregnant females will adopt the sternal decubitus position, while pregnant females will actively reject it, but this identification method has a reliability of approximately 80% (Pacheco-Fernandez, 2007). Early embryonic death occurs more frequently in alpacas and llamas than other livestock species. Estimates of 15–20% have been reported in North America. However, in South America, 50% embryo loss within the first thirty days is seen (Fowler and Bravo, 2010). Twin gestation is unusual in both llamas and alpacas (Sumar, 1996).

7. Early and parental behaviour

Appropriate and sufficient maternal care, and a strong, exclusive dam-young bond are crucial for the survival of the neonate, especially in extensive production systems (Redfearn et al., 2023). Pregnancy length in alpacas is 342–346 days, while in llamas it is 310–350 days, but may be significantly more variable outside South America, ranging from 320 to 400 days (Hallowell, 2019). Parturition in alpacas and llamas is generally quick, with more than 90% of births in alpacas and llamas occur between 07 and 13:00 h. This adaptation gives the new-born (or *crias*) the best chance to get warm and dry before the cold of night, when even in the summer, freezing temperatures are common at high altitudes. Camelids appear to be able to delay birthing for hours or days to avoid giving birth during the night or on cold days (Sumar, 1996). Exceptionally, nocturnal births have been reported especially in camelids reared outside the Andean region (Davis et al., 1997). The behavioural signs of preparation for parturition can last between 1 and 6 h, including separation of the mother from the rest of the herd and lack of interest in eating or grazing with the herd, vocalization through humming, restlessness, frequent visits to the latrine and sitting in sternal decubitus with hind legs out to the side (Whitehead, 2009).

The foetus is born in an anterior dorsosacral presentation and expulsion usually lasts 20–30 min, although in some cases it can last up to an hour. Most foetuses are expelled with the dam standing, adopting a labour position, which is similar to that of urinating (Hallowell, 2019). This has the advantage that the young are born more quickly and the umbilical cord is broken when the new-born falls (Aba et al., 2010). The new-born is covered by a thin translucent foetal epidermal membrane that adheres to the mucocutaneous junctions. This membrane can aid lubrication in the birth canal and also act as a windbreaker in the immediate postpartum period. It is usually shed during the first few hours of life when the *cria* dries out (Whitehead, 2009). After birth, maternal care of the young is minimal, neither llamas nor alpacas lick or groom their *cria*, and they do not eat or touch the placenta (Smith, 1985). The young must dry themselves, get up and look for the mother to nuzzle. Maternal care is limited to spitting or lunging to chase away unfamiliar animals and a reluctance to leave their young. Mothers also emit a low-frequency vocalization toward the new-born, and the *cria* responds with a version of this same call (Smith et al., 1994). Normal alpaca new-borns should weigh at least 5.5 kg and llama *cria* weigh 7 kg, although the average weight is probably closer to 7 and 9 kg respectively for alpaca and llama *cria* (Whitehead, 2009). In SADC the expulsion of the placenta normally occurs one hour after the birth of the foetus but may take up to 4 h. Retained placenta and dystocia are rare (1–5%). Common causes of dystocia are abnormal foetal position or presence, failure of cervical dilatation, twin pregnancies, uterine torsion, uterine inertia and uterine rupture (Miller et al., 2013).

Alpaca and llama offspring are considered precocial because they have visual, olfactory, gustatory, auditory capabilities and are able to stand up from birth and integrate into the activities of adult individuals within a few days (Broom and Fraser, 2015). Therefore. mothers usually show very little interest in the new-born until it first encounters the teat and attempts to suckle, which occurs within one hour after birth (Whitehead, 2009). Camelids have an epithelial microcotyledonous placenta that does not allow transfer of immunoglobulins from mother to foetus, so access to colostrum is a strategic aspect of neonatal welfare (Walker, 2022). Colostrum is normally consumed within the first hour after birth, then every 30 min for the first 4 h of life, and then every hour (Bravo, 2019). Pre-partum colostrum leakage or furtive suckling of other *crias* often affects the quantity and quality of colostrum available to the new-born (Walker, 2022). In addition to access to colostrum and good nutritional management of the mother, a vital aspect for the survival of neonates is protection against extreme temperatures (Gómez-Quispe et al., 2022).

Typically, the first few encounters with the udder are unsuccessful and the *cria* may switch teats until it receives colostrum and success seems to be expressed by the *cria* lifting its tail. Females verify by scent that the neonate is theirs and reject strange young by spitting or threats (Aba et al., 2010). Meconium should be expelled within 18–20 h postpartum (Whitehead, 2009). When the neonate has been resting for a long time, the mother starts sniffing it to stimulate sucking. However, the *cria* usually starts suckling without any stimulation. The suckling period is determined by the mother, pulling away or pushing her *cria* away when she is ready to stop suckling (Aba et al., 2010). At 6 months of age the *crias* are very independent and consume grass well, so weaning in traditional farming systems takes place between 6 and 8 months of age (Ayala-Vargas, 2018). In these systems, animals can be weaned using two different techniques: Placing a protector or harness on the udder for 21 days so that the *crias* cannot suckle; or separating the mothers from the *crias* of the original herd for 21 days, after which the *crias* can be re-integrated into the herd. In both techniques, the objective is to inhibit the suckling behaviour of the *cria* (INIA, 2000). During weaning, alpacas have elevated concentrations of cortisol that are maintained until day 3 after weaning, and then by day 5, cortisol decreases to basal values (Bravo et al., 2001). If they are not weaned, *crias* can continue to suckle until one and a half years of age (Ayala-Vargas, 2018).

Although information on orphaned offspring and maternal mortality is limited, a study of 660 alpacas from traditional systems in the Peruvian plateau reported a prevalence of dystocic birth mortality of 4.3% (n = 35) (Paredes et al., 2009). Offspring may be orphaned or simply require hand-rearing due to lack of milk production or, very rarely, due to maternal rejection. Goat or cow milk has been used effectively as a substitute (Tibary et al., 2014). High mortality due to hypothermia and pneumonia of *crias* within the first 3–4 months of life is one of the major problems affecting the profitability of alpaca raising (Martín-Espada et al., 2010). In this sense, Valenzuela et al. (2021) in a study in the Peruvian plateau with 150 alpaca *crias*, demonstrated that the use of thermal vests on the *crias* achieved 100% survival during the first 3 months of life, compared to *crias* housed in roofed pens (76%) or unroofed pens (64%).

8. Human-animal relationships and handling

The human-animal relationship (HAR) is dynamic and multifactorial, defined by mutual perception between animals and humans and reflected by their behaviour and feedback (Waiblinger et al., 2006). As in other domestic livestock, llamas have the ability to discriminate between unfamiliar and familiar humans, with a tendency to experience fear and avoidance towards strangers (Taylor and Davis, 1996). In both alpacas and llamas, fearful and aggressive behaviour towards humans includes spitting, biting, various vocalizations (squealing and/or howling, snorting and/or snapping), kicking, deliberate collapse (abruptly lying on the belly on the ground) and behavioural freezing (Windschnurer et al., 2020). Llamas and alpacas accustomed to people will generally not spit at humans (Gegner and Sharp, 2012). Body language is an important indicator for predicting habitual or sporadic HAR. Especially ear position and its combination with head position are predictive indicators of a positive or negative encounter with a human, and body position and tail are complementary signals (Fig. 3). For example, according to Kapustka and Budzyńska (2021), raised ears pointing toward the human, the neck and body forming a 90° angle, and the tail loosely downward are signals of interest and curiosity and would be a prelude to a positive interaction. Anxious or fearful animals will have their ears laid back, with the head lowered and the tail slightly raised. If ears are laid back, with the head raised, usually accompanied by the tail in a horizontal position, this may be a warning sign prior to defensive aggression by spitting.

Human contact with the young, especially SADC males, should be limited to avoid later abnormal behaviour such as Berserk syndrome (Tibary et al., 2014). This behavioural disorder usually arises between the first and third year of life, and is a product of inadequate and inadvertent over-socialization with humans when the animal is young, especially in bottle-fed neonates (Ball et al., 2015). One of the proposed causal mechanisms is that bottle-fed offspring imprint on human handlers, with the result that aggressive and sexual behaviours are directed toward humans when the camelid reaches sexual maturity (Bedenice and Whitehead, 2016). Males suffering from this condition may exhibit dangerous behaviours towards humans, so they are usually euthanized. Females can also suffer from this syndrome, but their behaviour is usually limited to spitting and difficult handling (Ball et al., 2015). In this context, there has been a trend to train SADCs to improve handling.

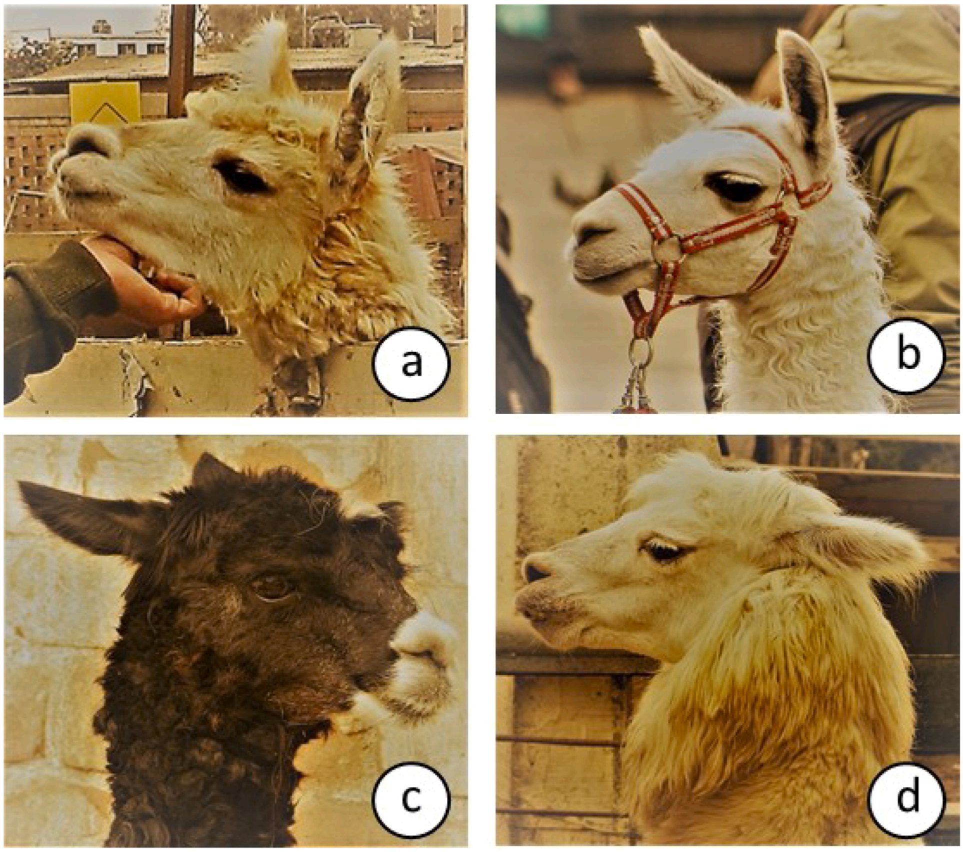

Fig. 3. Ear and head position are predictors of HAR in SADCs. a) Positive tactile interaction human-alpaca; b) Neutral interaction with humans, note the ears and head of a llama in surveillance position; c) Anxiety and fear in a young alpaca prior to handling; and d) Warning signs prior to defensive aggression by spitting in an adult alpaca.

Training techniques that rely on force or aggression make the animals dangerously aggressive towards people and they selectively obey humans who have "tamed" them out of fear (Bennett, 2022). These animals are especially dangerous with children, and when aggression becomes idiopathic the solution is often euthanasia. In contrast, positive reinforcement training has been used successfully for handling, shearing, loading/unloading trucks and clinical procedures (Bennett, 2014). Moreover, Windschnurer et al. (2021) found that gentle tactile, auditory and visual handling is related to calmer camelids, as shown by of the lack of signs of fear and easier handling. However, according to farmers' perceptions, a frightened SADC will avoid contact with the handler, and the establishment of a positive relationship between handler and animal is impossible, until the fear response has dissipated (Kapustka and Budzyńska (2021). HAR interactions can be improved by getting animals used to human contact, using handling procedures, improving handler skills and facility design (Miranda-de la Lama et al., 2022). Ideally, farm facilities could be used to create a series of enclosures, such as pens, so that the whole group or herd can be captured at the same time, and then separated into smaller groups (Anderson, 2013). Where only a single animal within a herd needs to be captured, the whole group should be captured first (Fowler, 2011). The use of halters is only recommended for very specific management practices, such as physical restraint and loading/unloading into a truck (Jones, 2013), and should not be used on a daily basis because camelids are nasal breathers. Care must be taken to avoid blocking the nostrils as this can cause sudden death (Bennett, 2014). Llamas tend to be more accepting of the placement and use of halters than alpacas (Fowler, 2011). Some authors recommend bandaging the neck, so that animals are less likely to be injured during restraint. In addition, if the animal is very reactive, it is possible to place a hood to obstruct the field of vision (Turner, 2014) or a halter and a towel fixed over the muzzle to prevent spitting (Jones, 2013).

Unlike equids and dogs, alpacas are cognitively flexible in spatial problem solving. They can change a learned route to access a reward (i.e. food), using other alternatives. This ability may have arisen since alpacas have had to adapt to challenging environments in which the quantity and quality of resources have frequent variations (Abramson et al., 2018). This capacity must be taken into account in terms of training, management, and facility design. Training, adapting or habituating animals to handling and loading procedures can reduce fear and improve camelids' tolerance to new situations, especially if this training is carried out gradually through short sessions (Turner, 2014). To this end, leading animals through the ramp, tethering, handling and touching them on the neck and feet should be a routine activity during the production period. (Miranda-de la Lama et al., 2022).

Interestingly, it has been in Europe, most notably Austria where more scientific analyses of welfare and HAR have been carried out with alpacas and llamas. For example, Windschnurer et al. (2020) note that in Europe, alpacas can be kept for fibre but also in animal-assisted activities like trekking or just as a companion or pet. Their study found that gentle handling early on in life had beneficial effects later on, making handling easier. However, as alpacas or llamas get older, some individuals may show signs of aggressive behaviour towards caretakers such as biting, bumping or kicking. Windschnurer et al. (2020) examined the reaction to handling in 81 alpacas and 35 llamas over a period of 3–4 min. They noted, among other characteristics, the effort needed to lead the animals (by a stranger, but in the presence of usual handlers), any balking or kicking, spitting etc., in addition to declarations by the owners about how the animals were treated at an early age. Overall, it was found that those animals that had been handled gently at an early age, had higher scores for docility.

Although most production systems for alpacas and llamas are quite extensive in nature, there are moments of more intense HAR, one of the most intense being during shearing. In the Latin American context, however, few systematic studies have been made of the effect of shearing on alpacas and llamas or their subsequent behaviour and reaction to humans (Miranda-de la Lama et al., 2022). More recently, increased attention is being paid to the effects of shearing on animal welfare, with best practice guidelines being produced for shearers (e.g., Peruvian Technical Standard, Good practices for shearing and handling of alpaca fibre fleece; NTP, 2019). Recently, in a study conducted in Peru, Kohl et al. (2023) observed in alpacas that after shearing, only feeding frequency increased, while other basic activities such as walking, standing, lying down with or without rumination were not affected. While in a European study, Waiblinger et al. (2020), specifically analysed the effects of shearing while keeping the animals standing up, lying down or on a table. Previous research in wild counterparts, guanacos and vicunas, indicates that welfare can be affected by the capture method and that the longer the capture and shearing process, the greater the stress (Arzamendia et al., 2010; Taraborelli et al., 2011), even causing the disorganization of family groups and causing a high percentage of mothers to subsequently lose their offspring (Sarno et al., 2009; Quispe et al., 2022). After shearing, all alpacas tend to feed less and ruminate less, while remaining standing and increasing levels of affiliative social interactions. When distressed, alpacas can moan or scream and occasionally growl, but, in the study by Waiblinger et al. (2020) fewer animals screamed when sheared standing up. Among the animals that screamed, there appeared to be a direct link with restraint and the noise from the clipper, since screaming tended to stop when the clipper was turned off. Ideally, positive conditioning could be used to habituate alpacas to being sheared without restraint, but that is not always possible. Lifting an alpaca off the ground to place it on a table may be more stressful than forcing it to lie down, a natural defence behaviour in SADC.

9. Future insights

The present bibliographic review relied on two main sources of scientific information on SADCs. One originating from countries where SADCs are not native, especially the European Union, USA and Australia. That information has been generated especially by clinical veterinarians and is related to behavioural, clinical and surgical aspects derived from the acute and chronic effects of the translocation of camelids to environmental conditions (climate and altitude) that are different from their native habitat. Under those production systems, there is an increasing interest in how handling and shearing stress may affect animal welfare. The second source of information comes from South America, where Peruvian and Bolivian studies have focused on aspects of breeding, husbandry, reproduction, fibre production and preventive health of SADCs, where the approach to behaviour and welfare is transversal to these topics. In Argentina and Chile, studies mostly have focused on conservation, behaviour and management, especially of wild camelids. From the above sections it is evident that more is known about the basic biology of camelids, including sexual and maternal behaviour, than other aspects of sensory systems, cognition, or maintenance and social behaviours. Research is needed on how different handling procedures, such as shearing, transport, pre-slaughter handling and slaughter, affect the welfare of SDAC and which indicators can be used reliably by producers.

In the future, in the context of international trade and long production chains, where trust needs to be instilled in the end consumer (Richards et al. 2011), applied research will most probably focus on operational welfare indicators of commercially produced llamas and alpacas, both on the farm and during different handling procedures. Presently, several non-governmental organizations and welfare assurance programs have begun to work on protocols which will help to certify welfare-friendly production systems, and handling practises such as shearing or slaughter. In South America, however, any certification process must consider impacts on social and commercial aspects on livelihoods of small peasant farms (Markemann et al., 2009), which, for example in Peru, represent, collectively, more than 80% of total production. As underlined by Main et al. (2014), any animal welfare certification scheme should consider aspects related to continuous improvement, targeted assessment and support, as well as being open to external scrutiny. Current production schemes for llamas and alpacas in South America may not lend themselves easily to such principles at the moment, but efforts are being made in the direction.

10. Conclusions

Although South American domestic camelids have a long history as farm animals in the Andean region, there are few scientific records about their welfare, especially from a behavioural perspective. Llamas and alpacas are highly valued by owners and their welfare is primordial, but objective ethological studies are scare. Based on our review of the literature, SADC are well adapted to extensive production at high altitudes, but the current tendency is towards more intensive production, especially for meat and fibre. Under those conditions, it becomes more important to understand their sensory and communication systems and social behaviour, which have all been reviewed here. In most cases, alpacas and llamas avoid being isolated from the group, which makes some handling procedures more difficult, such as shearing, but methods have been used to improve their welfare under those circumstances. The HAR is multifactorial but the production sector would benefit from using welfare-friendly handling techniques and equipment, as more and more knowledge is being acquired in recent years.

Declaration of Competing Interest

None of the authors has any financial or personal relationships that could inappropriately influence or bias the content of the manuscript.

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References

Aba, M.A., Bianchi, C., Cavilla, V., 2010. South American camelids. Behav. Exot. Pets 157–167.

Abramson, J.Z., Soto, D., Zapata, S., Lloreda, M.V.H., 2018. Spatial perseveration error by alpacas (Vicugna pacos) in an A-not-B detour task. Anim. Cogn. 21, 433–439.

Anderson, D.E., 2013. Behavior and capture techniques. In: Anderson, D.E., Jones, M.L., Miesner, M.D. (Eds.), Veterinary techniques for llamas and alpacas. John Wiley & Sons, Ames, IA, pp. 2–7.

Anello, M., Daverio, M.S., Di Rocco, F., 2022. Genetics of coat color and fiber production traits in llamas and alpacas. Anim. Front 12 (4), 78–86.

Arzamendia, Y., Bonacic, C., Vilá, B., 2010. Behavioural and physiological consequences of capture for shearing of vicuñas in Argentina. Appl. Anim. Behav. Sci. 125 (3–4), 163–170.

Ayala-Vargas, C., 2018. South American camelids. Rev. Invest. Innov. Agrop. Rec. Nat. 5, 7–12.

Azémard, C., Dufour, E., Zazzo, A., Wheeler, J.C., Goepfert, N., Marie, A., Zirah, S., 2021. Untangling the fibre ball: Proteomic characterization of South American camelid hair fibres by untargeted multivariate analysis and molecular networking. J. Proteom. 231, 104040.

Balcarcel, A.M., Sánchez-Villagra, M.R., Segura, V., Evin, A., 2021. Singular patterns of skull shape and brain size change in the domestication of South American camelids. J. Mammal. 102 (1), 220–235.

Ball, S.R., Way, K., Schleining, J.A., Millman, S.T., 2015. survey-based examination of demographics, potential causes and treatments of aberrant behavior syndrome (berserk male syndrome) in camelids. Anim. Indust. Rep. 661 (1), 70.

Barreta, J., Iñiguez, V., Saavedra, V., Romero, F., Callisaya, A.M., Echalar, J., Arranz, J. J., 2012. Genetic diversity and population structure of Bolivian alpacas. Small Rumin. Res. 105 (1–3), 97–104.
Bedenice, D., Whitehead, C., 2016. A systematic approach to the neurological examination of llamas and alpacas. Livest 21 (5), 308–313.
Bennett, M.M., 2014. Camelid management, handling techniques and facilities. In: Cebra, C., Anderson, D., Tibary, A., Van Saun, R., Johnson Larue, W. (Eds.), Llama and alpaca care: medicine, surgery, reproduction. Elsevier, St.-Louis, MI, pp. 22–50.
Bennett, M.M., 2022. South american camelid behavior and the CAMELIDynamics approach to handling. In: Niehaus, A.J. (Ed.), Medicine and Surgery of Camelids. John Wiley & Sons, pp. 19–54.
Biasutti, S.A., Dart, A.J., 2019. Suspected capture myopathy in an alpaca (Vicugna pacos) following a dog attack. N. Z. Vet. J. 67, 52–54.
Björklund, C., 2014. Diseases and causes of death among camelids in Sweden: a retrospective study of necropsy cases 2001–2013. BSc. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
Blank, D.A., 2021. Artiodactyl vocalization. In: Rosenfeld, C.S., Hoffmann, F. (Eds.), Neuroendocrine Regulation of Animal Vocalization: Mechanisms and Anthropogenic Factors in Animal Communication, pp. 159–188.
Bonacic, C., 2011. South American camelids. In: Webster, J., Margerison, J. (Eds.), Management and welfare of farm animals: UFAW farm handbook. Wiley-Blackwell, pp. 477–499.
Bravo, P.W., 2014. In: Cebra, C., Anderson, D., Tibary, A., Van Saun, R., Johnson, L.W. (Eds.), Reproductive Anatomy and Physiology in the Male. Llama and alpaca care. Elsevier Health Sciences.
Bravo, P.W., 2015. Chapter 60 – Camelidae. In: Miller, R.E., Fowler, M. (Eds.), Fowler's Zoo and Wild Animal Medicine, Volume 8. WB Saunders.
Bravo, P.W., 2019. The alpaca cria, clinical and immunological aspects. In: Gutiérrez, C., McKenna, L., Niznikowski, R., Wurzinger, M. (Eds.), Adv. Fibre Prod. Sci. South Am. Camelids Other Fibre Anim. 195.
Bravo, P.W., Fowler, M.E., 2008. Chapther 34 order artiodactyla, family camelidae (Guanacos, Vicuñas). In: Fowler, M., Cubas, Z.S. (Eds.), Biology, medicine, and surgery of South American wild animals. John Wiley & Sons.
Bravo, P.W., Skidmore, J.A., Zhao, X.X., 2000. Reproductive aspects and storage of semen in Camelidae. Anim. Reprod. Sci. 62 (1–3), 173–193.
Bravo, P.W., Garnica, J., Aviles, E., 2001. Cortisol concentrations in the perinatal and weaning periods of alpacas. Anim. Reprod. Sci. 67 (1–2), 125–129.
Bravo, P.W., Moscoso, R., Alarcon, V., Ordoñez, C., 2002. Ejaculatory process and related semen characteristics. Arch. Androl. 48 (1), 65–72.
Bravo-Cuevas, V.M., Jiménez-Hidalgo, E., Cuevas-Ruiz, G.E., Cabral-Perdomo, M.A., 2012. A small camelid Hemiauchenia from the Late Pleistocene of Hidalgo, central Mexico. Acta Palaeontol. Pol. 57 (3), 497–508.
Broom, D.M., Fraser, A.F., 2015. Domestic animal behaviour and welfare. Cabi, UK.
Carmanchahi, P.D., Ovejero, R., Marull, C., Lopez, G.C., Schroeder, N., Jahn, G.A., Novaro, A.J., Gand, C., Somoza, G.M., 2011. Physiological response of wild guanacos to capture for live shearing. Wildl. Res. 38, 61–68.
Carrasco, R.A., Pezo, S., Adams, G.P., 2021. Evidence for the LH-releasing pathway of seminal plasma NGF in male camelids. Theriogenology 164, 100–104.
Casaverde, J., Huanca, T., 1985. Alpaca farmer's communities. Minka 16, 1–32.
Castellaro, G., Ullrich, T., Wackwitz, B., Raggi, A., 2004. Botanical composition of the diet of alpacas (Lama pacos L.) and llamas (Lama glama L.) in two seasons of the year, in altiplanic grasslands of a sector of the Parinacota Province Chile. Agric. Téc 64 (4), 353–363.
Castro-Bedriñana, J., Chirinos Peinado, D., Rojas Pérez, R., 2017. Early learning to eat concentrate in Huacaya alpacas. Rev. Invest. Vet. Peru. 28 (1), 71–77.
Cebra, C., 2014. Chapter 40. Disorders of the digestive system. In: Cebra, C., Anderson, D.E., Tibary, A., Van Saun, R.J., Johnson, L.W. (Eds.), Llama and Alpaca Care-E-Book: Medicine, Surgery, Reproduction, Nutrition, and Herd Health, pp. 477–536.
Chamut, S., Cancino, A.K., Black-Decima, P., 2016. The morphological basis of vicuña wool: skin and gland structure in Vicugna vicugna (Molina 1782). In: Small Rumin. Res, 137, pp. 124–129.
Correa, L.A., Zapata, B., Samaniego, H., Soto-Gamboa, M., 2013. Social structure in a family group of Guanaco (Lama guanicoe, Ungulate): Is female hierarchy based on 'prior attributes' or 'social dynamics'?. In: Behav. Process, 98, pp. 92–97.
Craig, A.D., 2003. Pain mechanisms: Labeled lines versus convergence in central processing. Annu. Rev. Neurosci. 26, 1–30.
D'Alterio, G.L., Knowles, T.G., Eknaes, E.I., Loevland, I.E., Foster, A.P., 2006. Postal survey of the population of South American camelids in the United Kingdom in 2000/01. Vet. Rec. 158 (3), 86–90.
Davis, G.H., Dodds, K.G., Moore, G.H., Bruce, G.D., 1997. Seasonal effects on gestation length and birth weight in alpacas. Anim. Reprod. Sci. 46 (3–4), 297–303.
Diaz-Maroto, P., Rey-Iglesia, A., Cartajena, I., Núñez, L., Westbury, M.V., Varas, V., Hansen, A.J., 2021. Ancient DNA reveals the lost domestication history of South American camelids in Northern Chile and across the Andes. Elife 10, e63390.
Duncanson, G.R., 2012. Veterinary treatment of llamas and alpacas. CABI, Oxfordshire.
El Zawam, A., Tibary, A., Patino, C., 2020. Basal levels and hCG responses of serum testosterone and estrogen in male alpacas. Front. Vet. Sci. 7, 595856.
Enke, N., Brinkmann, L., Runa, R.A., Südekum, K.H., Tholen, E., Gerken, M., 2022. Drinking behaviour of llamas (Lama glama) in choice tests for fresh or saline water. Small Rumin. Res. 216, 106806.
Erdoğan, S., Arias, Villar, Pérez, W, S., 2016. Morphofunctional structure of the lingual papillae in three species of South American Camelids: alpaca, guanaco, and llama. Microsc. Res. Tech. 79 (2), 61–71.
Esteban, L.R., Thompson, J.R., 1988. The digestive system of New World camelids-common digestive diseases of llamas. IOWA State Univ. Vet. 50 (2), 9.
Estévez-Moreno, L.X., Miranda-de la Lama, G.C., Miguel-Pacheco, G.G., 2022. Consumer attitudes towards farm animal welfare in Argentina, Chile, Colombia, Ecuador, Peru and Bolivia: a segmentation-based study. Meat Sci. 187, 108747.
Fan, R., Gu, Z., Guang, X., Marín, J.C., Varas, V., González, B.A., Wheeler, J.C., Hu, Y., Li, E., Sun, X., Yang, X., Zhang, C., Gao, W., He, J., Munch, K., Corbett-Detig, R., Barbato, M., Pan, S., Zhan, X., Bruford, M.D., Dong, C., 2020. Genomic analysis of the domestication and post-Spanish conquest evolution of the llama and alpaca. Genome Biol. 21, 1–26.
Fernandez-Baca, S., Madden, D.H.L., Novoa, C., 1970. Effect of different mating stimuli on induction of ovulation in the alpaca. Reprod 22 (2), 261–267.
Fowler, M., 2011. Medicine and surgery of camelids. John Wiley & Sons, Ames, IA.
Fowler, M.E., 2008. Behavioral clues for detection of illness in wild animals: models in camelids and elephants. In: Fowler, M.E., Miller, E.R. (Eds.), Zoo and wild animal medicine current therapy-e-book. Elsevier, St.-Louis, MI, pp. 33–49.
Fowler, M.E., Bravo, W.P., 2010. 17 Reproduction. In: restraint and handling. In: Fowler, M.E. (Ed.), Medicine and surgery of camelids. John Wiley & Sons, Ames, IA, pp. 429–478.
Franklin, W.L., Johnson, W.E., 1994. Hand capture of newborn open-habitat ungulates: the South American guanaco. Wildl. Soc. Bull. 22, 253–259.
Gade, D.W., 2013. Llamas and alpacas as" sheep" in the colonial Andes: zoogeography meets Eurocentrism. J. Lat. Am. Geogr. 221–243.
Gandarillas, V., Jiang, Y., Irvine, K., 2016. Assessing the services of high mountain wetlands in tropical Andes: a case study of Caripe wetlands at Bolivian Altiplano. Ecosyst 19, 51–64.
Gauly, M., Vaughan, J., Hogreve, S.K., Erhardt, G., 2005. Brainstem auditory-evoked potential assessment of auditory function and congenital deafness in llamas (Lama glama) and alpacas (lama pacos). J. Vet. Intern. Med 19, 756–760.
Gegner, L., Sharp, H., 2012. Llamas and Alpacas on the Farm. Butte, MT: ATTRA Sustainable.
Gionfriddo, J.R., 2010. Ophthalmology of South american camelids. Vet. Clin. North Am. Food Anim. 26 (3), 531–555.
Gómez-Quispe, O.E., Rodríguez, E.L., Benites, R.M., Valenzuela, S., Moscoso-Muñoz, J., Ibañez, V., Youngs, C.R., 2022. Analysis of alpaca (*Vicugna pacos*) cria survival under extensive management conditions in the high elevations of the Andes mountains of Peru. Small Rumin. Res., 106839
Goñalons, G.L.M., 2008. Camelids in ancient Andean societies: a review of the zooarchaeological evidence. Quat. Int. 185 (1), 59–68.
Grubb, T., 2014. Pain management in camelids: systemic techniques. In: Cebra, C., Anderson, D., Tibary, A., Van Saun, R., Johnson Larue, W. (Eds.), Llama and alpaca care: medicine, surgery, reproduction, nutrition, and herd health. Elsevier, St.- Louis, MI, pp. 618–624.
Guamán, M., 2018. Andean camelids (wiwakuna tawantinsuyu runakunapak kawsaypi). Rev. Chakiñan Cien. Soc. Hum. 5, 5–17.
Gunsser, I., 2019. Teeth in camelids: myths, facts and problems. In: Gutiérrez, C., McKenna, L., Niznikowski, R., Wurzinger, M. (Eds.), Advances in Fibre Production Science in South American Camelids and other Fibre Animals, 229.
Hallowell, G.D., 2019. Old and new world camelids. In Veterinary Reproduction and Obstetrics. WB Saunders, pp. 670–682.
Hilton, C.D., Pugh, D.G., Wright, J.C., Waldridge, B.M., Simpkins, S.A., Heath, A.M., 1998. How to determine and when to use body weight estimates and condition scores in llamas. Veterinary medicine, Edwardsville, Kan.(USA).
Heffner, R.S., Koay, G., Heffner, H.E., 2014. Hearing in alpacas (Vicugna pacos): Audiogram, localization acuity, and use of binaural locus cues. The Journal of the Acoustical Society of America 135 (2), 778–788.
Hund, A., Wittek, T., 2018. Abomasal and third compartment ulcers in ruminants and south American camelids. Vet. Clin. North Am. Food Anim. 34, 35–54.
INIA., 2000. Weaning, Alpaca husbandry issue 7. Instituto Nacional de Investigación Agraria – INIA. 20. Pp11.
Johnson, L.W., 1994. Update. Llama nutrition. Vet. Clin. North Am. Food Anim. 10 (2), 187–201.
Jones, M., 2013. Haltering. In: Anderson, D.E., Jones, M.L., Miesner, M.D. (Eds.), Veterinary techniques for llamas and alpacas. John Wiley & Sons, Ames, IA, pp. 11–13.
Kadwell, M., Fernandez, M., Stanley, H.F., Baldi, R., Wheeler, J.C., Rosadio, R., Bruford, M.W., 2001. Genetic analysis reveals the wild ancestors of the llama and the alpaca. Proc. R. Soc. B Biol. 268 (1485), 2575–2584.
Kapustka, J., Budzyńska, M., 2021. Human ability to interpret alpaca body language. J. Vet. Behav. 42, 16–21.
Kats, L.B., Dill, L.M., 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience 5, 361–394.
Kohl, T., Wurzinger, M., Reynoso, G.G., Waiblinger, S., 2023. Reactions of Alpacas to Shearing and Accompanying Procedures. Small Ruminant Research 219, 106885.
Lichtenwalner, A.B., Woods, G.L., Weber, J.A., 1998. Male llama choice between receptive and nonreceptive females. Appl. Anim. Behav. Sci. 59 (4), 349–356.
Llanos, A.J., Riquelme, R.A., Herrera, E.A., Ebensperger, G., Krause, B., Reyes, R.V., Hanson, M.A., 2007. Evolving in thin air—lessons from the llama fetus in the altiplano. Respir. Physiol. Neurobiol. 158 (2–3), 298–306.
Mader, C., Hölzl, S., Heck, K., Reindel, M., Isla, J., 2018. The llama's share: highland origins of camelids during the Late Paracas period (370 to 200 BCE) in south Peru demonstrated by strontium isotope analysis. J. Archaeol. Sci. Rep. 20, 257–270.
Main, D.C.J., Mullan, S., Atkinson, C., Cooper, M., Wrathall, J.H.M., Blokhuis, H.J., 2014. Best practice framework for animal welfare certification schemes. Trend Food Sci. Technol. 37 (2), 127–136.
Mamani-Linares, L.W., Cayo, F., Gallo, C., 2014. Carcass characteristics, meat quality and chemical composition of llama meat: a review. Rev. Invest. Vet. Peru. 25 (2), 123–150.

Mamani-Mondragón, C.V., 2014. Susceptibility of the corpus luteum to prostaglandin F2a action in alpacas induced to ovulate with seminal plasma. Bachelor Thesis. Universidad Nacional Mayor de San Marcos. Lima, Perú.
Markemann, A., Stemmer, A., Siegmund-Schultze, M., Piepho, H.P., Zárate, A.V., 2009. Stated preferences of llama keeping functions in Bolivia. Livest. Sci. 124 (1–3), 119–125.
Matthews, P.T., Barwick, J., Doughty, A.K., Doyle, E.K., Morton, C.L., Brown, W.Y., 2020. Alpaca field behaviour when cohabitating with lambing ewes. Animals 10, 1605.
McLean, K., Niehaus, A.J., 2022. General biology and evolution. In: Niehaus, A.J. (Ed.), Medicine and Surgery of Camelids. John Wiley & Sons, pp. 1–18.
Metzler, A., 2020. Diagnosis and treatment of common ophthalmic disorders in South American camelids. Livest 25 (3), 156–162.
Miller, B.A., Brounts, S.H., Anderson, D.E., Devine, E., 2013. Cesarean section in alpacas and llamas: 34 cases (1997–2010). J. Am. Vet. Med. Assoc. 242 (5), 670–674.
Miranda-de la Lama, G.C., Mamani-Linares, W., Estévez-Moreno, L.X., 2022. Chapter 9: Species destined for non-traditional meat production: 2. Goats and South American domestic camelids. Preslaughter handling and slaughter of meat animals. Wageningen Academic Publishers, pp. 840–844.
Miranda-de la Lama, G. C., Mattiello, S., 2010. The importance of social behaviour for goat welfare in livestock farming. Small Rumin. Res. 90 (1–3), 1–10.
Montelli, S., Graïc, J.M., Ruiz, J.A., Stelletta, C., Peruffo, A., 2020. Neurochemical characterization of the hypothalamus of the early fetal and newborn alpaca Vicugna pacos. Anat. Rec. 303 (11), 2865–2877.
Neubert, S., von Altrock, A., Wendt, M., Wagener, M.G., 2021. Llama and alpaca management in Germany—Results of an online survey among owners on farm structure, health problems and self-reflection. Animals 11 (1), 102.
NTP, 2019. Norma Técnica Peruana 231.370:2019. Domestic Camelids. Good shearing and fleece management practices for alpaca fibre. Instituto Nacional de Calidad - Inacal, Lima. Perú.
O'Shaughnessy, N., 2008. Romancing alpacas: a commentary. J. Bus. Res. 61 (5), 509–511.
Pacheco-Fernandez, L.A., 2007. Study of semen quality and effect on the fertility of llamas in a controlled mating system (Lama glama). Bachelor Thesis. Universidad Mayor de San Andrés, La Páz, Bolivia.
Panebianco, A., Gregorio, P.F., Ovejero, R., Marozzi, A., Ruiz Blanco, M., Leggieri, L.R., Carmanchahi, P.D., 2021. Male aggressiveness in a polygynous ungulate varies with social and ecological context. Ethol 127 (1), 68–82.
Paredes, J.M., Condemayta, Z.C., Charaja, L.C., 2009. Causes of mortality of alpacas in three main centers of production located in dry and humid fist of the Puno department. Rev. Electron. De. Vet. 10 (8), 1–13.
Pizzaro, D.M., Gutiérrez, G.A., Ñaupari, J.A., Wurzinger, M., 2019. Performance Evaluation of Llama, Alpaca and Sheep Herds of a Community in Pasco, Peru. Gutiérrez, C., McKenna, L., Niznikowski, R., Wurzinger, M. (eds.) Advances in Fibre Production Science in South American Camelids and other Fibre Animals, 83.
Plummer, P.J., Schleining, J.A., 2013. Assessment and management of pain in small ruminants and camelids. Vet. Clin. North Am. Food Anim. 29, 185–208.
Pollard, J.C., Littlejohn, R.P., Scott, I.C., 1994. The effects of mating on the sexual receptivity of female alpacas. Anim. Reprod. Sci. 34 (3–4), 289–297.
Pollard, J.C., Littlejohn, R.P., Moore, G.H., 1995. Seasonal and other factors affecting the sexual behaviour of alpacas. Anim. Reprod. Sci. 37 (3–4), 349–356.
Provenza, F.D., Balph, D.F., 1987. Diet learning by domestic ruminants: theory, evidence and practical implications. Appl. Anim. Behav. Sci. 18 (3–4), 211–232.
Quispe, C., Ñaupari, J., Distel, R.A., Flores, E., 2021. Feeding selection of sheep and alpaca on puna tussock rangelands grazed previously by cattle. Small Rumin. Res. 197, 106349.
Quispe, E., Siguas, O., Espinoza, M., Arana, W., Contreras, J., Cassinello, J., Bartolomé, J., 2022. Group structure in vicuña (Vicugna vicugna mensalis) subject to chaku management in central Andes, Peru. Small Rumin. Res. 210, 106661.
Redfearn, A., Janodet, E., McNally, J., Brewer, H., Doyle, E., Doyle, R., Schmoelzl, S., 2023. Postnatal maternal behaviour expression depends on lambing difficulty in Merino ewes. Theriogenology 196, 31–36.
Reiner, R.J., Bryant, F.C., 1986. Botanical composition and nutritional quality of alpaca diets in two Andean rangeland communities. J. Range Manag 39 (5), 424–427.
Richards, C., Lawrence, G., Burch, D., 2011. Supermarkets and agro-industrial foods: The strategic manufacturing of consumer trust. Food Cult. Soc. 14 (1), 29–47.
Riek, A., Stölzl, A., Marquina Bernedo, R., Ruf, T., Arnold, W., Hambly, C., Gerken, M., 2019. Energy expenditure and body temperature variations in llamas living in the High Andes of Peru. Sci. Rep. 9 (1), 1–11.
Ríos, M., Schlundt, F., Bryant, F., 1984. Behaviour of alpacas under four grazing intensities in the Southern Highlands of Peru. In: Fierro, I.C., Farfan, R. (Eds.), Research on pastures and forages. Texas Tech. Univ. Peru, pp. 36–54.
Rojas, D.A., Pérez, U.H., Llacsa, J., Roque, B., 2021. Effect of fibrous concentrate supplementation on reproductive performance of alpacas in the Peruvian altiplano. Rev. Invest. Vet. Peru. 32 (4), e20926.
San Martin, F., Bryant, F.C., 1989. Nutrition of domesticated South American llamas and alpacas. Small Rumin. Res. 2, 191–216.
San Martín, F., Van Saun, R.J., 2013. Applied digestive anatomy and feeding behavior. Llama and Alpaca Care: Medicine, Surgery, Reproduction Nutrition, and Herd Health, first ed. Elsevier Inc, pp. 51–58.
San-Martin, M., Copaira, M., Zuniga, J., Rodreguez, R., Bustinza, G., Acosta, L., 1968. Aspects of reproduction in the alpaca. Reprod 16 (3), 395–399.
Sarno, R.J., González, B.A., Bonacic, C., Zapata, B., O'Brien, S.J., Johnson, W.E., 2009. Molecular genetic evidence for social group disruption of wild vicuñas Vicugna vicugna captured for wool harvest in Chile. Small Rumin. Res. 84 (1–3), 28–34.
Schaffer, A., Caicoya, A.L., Colell, M., Holland, R., Ensenyat, C., Amici, F., 2020. Gaze following in ungulates: domesticated and non-domesticated species follow the gaze of both humans and conspecifics in an experimental context. Front. Psychol. 11, 604904.
Silva, N., Huanca, W.F., Medina, G., Huanca, W., 2020. Effect of seminal plasma, GnRH and follicular ablation on follicular dynamics in llamas (Lama glama). Rev. Invest. Vet. Peru. 31 (4).
Smith, C.L., Peter, A.T., Pugh, D.G., 1994. Reproduction in llamas and alpacas: a review. Theriogenology 41 (3), 573–592.
Smith, J.S., Schleining, J., Plummer, P., 2021. Pain management in small ruminants and camelids: analgesic agents. Vet. Clin. North Am. Food Anim. 37 (1), 1–16.
Smith, T.M., 1985. Reproduction in South American Camelids. IOWA State Univ. Vet. 47 (2), 6.
Smith-Davila, C.E., Mendoza Torres, G.J., Barbeito, C.G., Ghezzi, M.D., 2019. Evaluation of animal welfare conditions of South American camelids admitted to the Huancavelica municipal slaughterhouse. Peru. Rev. Mex. Cienc. Pecu. 10, 379–390.
Stanley, H.F., Kadwell, M., Wheeler, J.C., 1994. Molecular evolution of the family Camelidae: a mitochondrial DNA study. Proc. R. Soc. B 256 (1345), 1–6.
Sumar, J., 1988. Present and potential role of South American camelids in the high Andes. Outlook Agric. 17 (1), 23–29.
Sumar, J., 1991. Physiology of male reproduction and reproductive management. In: Advances and Perspectives in the Knowledge of South American Camelids. Fernández-Baca (Ed), FAO Santiago, Chile. pp 117- 137.
Sumar, J., 1996. Reproduction in llamas and alpacas. Anim. Reprod. Sci. 42 (1–4), 405–415.
Taraborelli, P., Ovejero, R., Schroeder, N., Moreno, P., Gregorio, P., Carmanchahi, P., 2011. Behavioural and physiological stress responses to handling in wild guanacos. J. Nat. Conserv 19 (6), 356–362.
Taraborelli, P., Gregorio, P., Moreno, P., Novaro, A., Carmanchahi, P., 2012. Cooperative vigilance: the guanaco's (Lama guanicoe) key antipredator mechanism. Behav. Proc. 91 (1), 82–89.
Taylor, A.A., Davis, H., 1996. The Response of llamas (Lama glama) to familiar and unfamilar humans. Int. J. Comp. Psychol. 9, 43–50.
Tibary, A., Vaughan, J., 2006. Reproductive physiology and infertility in male South American camelids: a review and clinical observations. Small Rumin. Res. 61 (2–3), 283–298.
Tibary, A., Johnson, L.W., Pearson, L.K., Rodriguez, J.S., 2014. Lactation and neonatal care. In: Cebra, C., Anderson, D., Tibary, A., Van Saun, R., and Johnson, L. W. (Eds.). Llama and Alpaca Care. Elsevier Health Sciences.
Travaini, A., Zapata, S.C., Bustamante, J., Pedrana, J., Zanón, J.I., Rodríguez, A., 2015. Guanaco abundance and monitoring in Southern Patagonia: distance sampling reveals substantially greater numbers than previously reported. Zool. Stud. 54 (1), 1–12.
Turner, A.A., 2014. Alpacas, llamas & guanaco. Welfare guide issued to form secondary legislation attached to the Animal Welfare Act 2006. British Alpaca Society, Exeter, UK, 60 pp.
Valenzuela, S., Benites, R.M., Moscoso-Muñoz, J.E., Youngs, C.R., Gómez-Quispe, O.E., 2021. Impact of cria protection strategy on post-natal survival and growth of alpacas (Vicugna pacos). Vet. Anim. Sci. 11, 100162.
Van Hoy, G., Marsh, A.E., Carman, M.K., 2022. External parasites. In: Niehaus, A.J. (Ed.), Medicine and Surgery of Camelids. John Wiley & Sons, pp. 174–223.
Van Saun, R.J., 2006. Nutritional diseases of South American camelids. Small Rumin. Res. 61 (2–3), 153–164.
Varas, V., Vásquez, J.P., Rivera, R., Longo, A., Valdecantos, P.A., Wheeler, J.C., Marín, J. C., 2020. Interbreeding among South American camelids threatens species integrity. J. Arid Environ. 181, 104249.
Vásquez, V.F., Redondo, R., Rosales, T.E., Dorado, G., Peiró, V., 2020. Osteometric and isotopic (δ13C and δ15N) evidence of Pre-Hispanic camelid-herd breeding in Moche site of "Huaca de la Luna" (North coast of Peru). J. Archaeol. Sci. Rep. 29, 102083.
Vater, A., Maierl, J., 2018. Adaptive anatomical specialization of the intestines of alpacas taking into account their original habitat and feeding behaviour. Anat. Rec. 301 (11), 1840–1851.
Vélez-Marroquín, V.M., Cabezas-Garcia, E.H., Antezana-Julian, W., Estellés-Barber, F., Franco, F.E., Pinares-Patiño, C.S., 2022. Design, operation, and validation of metabolism crates for nutrition studies in alpacas (Vicugna pacos). Small Rumin. Res. 209, 106660.
Vilá, B., Arzamendia, Y., 2020. South American Camelids: their values and contributions to people. 17, 707–724.
Wagener, M.G., Neubert, S., Punsmann, T.M., Wiegand, S.B., Ganter, M., 2021. Relationships between body condition score (BCS), FAMACHA©-score and haematological parameters in alpacas (Vicugna pacos), and llamas (Lama glama) presented at the veterinary clinic. Animals 11 (9), 2517.
Waiblinger, S., Baumgartner, J., Kiley-Worthington, M., Niebuhr, K., 2004. Applied ethology: the basis for improved animal welfare in organic farming. In: Vaarst, M. Roderick, S., Lund, V., Lockeretz, W. Animal health and welfare in organic agriculture. Pp.117–161.
Waiblinger, S., Boivin, X., Pedersen, V., Tosi, M.V., Janczak, A.M., Visser, E.K., Jones, R. B., 2006. Assessing the human–animal relationship in farmed species: a critical review. Appl. Anim. Behav. Sci. 101 (3–4), 185–242.
Waiblinger, S., Hajek, F., Lambacher, B., Wittek, T., 2020. Effects of the method of restraint for shearing on behaviour and heart rate variability in alpacas. Applied Animal Behaviour Science 223, 104918.
Walker, P.G., 2022. Neonatology. In: Niehaus, A.J. (Ed.), Medicine and Surgery of Camelids. John Wiley & Sons.
Wang, T., Hung, C.C., Randall, D.J., 2006. The comparative physiology of food deprivation: from feast to famine. Annu. Rev. Physiol. 68, 223–251.

Wheeler, J.C., 1995. Evolution and present situation of the South American Camelidae. Biol. J. Linn. Soc. 54, 271–295.
Wheeler, J.C., Russel, A.J.F., Redden, H., 1995. Llamas and alpacas: pre-conquest breeds and post-conquest hybrids. J. Archaeol. Sci. 22 (6), 833–840.
Whitehead, C.E., 2009. Management of neonatal llamas and alpacas. Vet. Clin. North Am. Food Anim. 25 (2), 353–366.
Willis, A.M., Mutti, D.O., Anderson, D.E., 2000. Refractive error in llamas and alpacas. In Proceedings 31st Annual Meeting Am. Col. Vet. Ophthalmol, Montreal, Canada. pp. 26.
Wilson, P.E., 1982. An analysis of male-male aggression in guanaco male groups, M.Sc. Thesis. Iowa State University.
Whitehead, C.E., Bedenice, D., 2009. Neurologic diseases in llamas and alpacas. Veterinary Clinics of North America: Food Animal Practice 25 (2), 385–405.
Windschnurer, I., Eibl, C., Franz, S., Gilhofer, E.M., Waiblinger, S., 2020. Alpaca and llama behaviour during handling and its associations with caretaker attitudes and human-animal contact. Appl. Anim. Behav. Sci. 226, 104989.
Windschnurer, I., Fischer, L., Yanagida, T., Eibl, C., Franz, S., Waiblinger, S., 2021. Caretaker attitudes and animal training are associated with alpaca behaviour towards humans - an online survey. Appl. Anim. Behav. Sci. 236, 105224.
Wurzinger, M., Gutiérrez, G., 2022. Alpaca breeding in Peru: from individual initiatives towards a national breeding program? Small Rumin. Res., 106844
Yacobaccio, H.D., 2021. The domestication of South American camelids: a review. Anim. Front 11 (3), 43–51.
Yacobaccio, H.D., Vilá, B.L., 2016. A model for llama (Lama glama Linnaeus, 1758) domestication in the southern Andes. Anthropozoologica 51 (1), 5–13.
Gerken, M., Brinkmann, L., Runa, R.A., Riek, A., 2019. In: Gutiérrez, C., McKenna, L., Niznikowski, R., Wurzinger, M. (Eds.), Water Metabolism in South American Camelids, Advances in Fibre Production Science in South American Camelids and other Fibre Animals, 267.