

Relationships between integumental characteristics and thermoregulation in South American camelids

M. Gerken[†]

Department of Animal Sciences, Göttingen University, Albrecht-Thaer-Weg 3, 37075 Göttingen, Germany

(Received 27 April 2009; Accepted 9 October 2009; First published online 20 November 2009)

Hair fibre is regarded as a unique mammalian feature with an important role for endothermy. Artificial selection for hair characteristics resulted in marked changes with regard to follicle number, type, distribution, growth and natural shedding. This review focuses on the fine fibre-producing South American camelids (SACs) and the relationship between their hair coat and thermoregulation. SACs have developed several special integumental characteristics. While the hair coat of the wild lamoids vicuña (Vicugna vicugna) and guanaco (Lama guanicoe) is formed by two types of hair (the coarse outer guard hairs and a finer undercoat), the domesticated llamas (Lama glama) and alpaca (Lama pacos) exhibit variably double coat and predominantly single coat, respectively. The distribution of the hair coat across the body is not homogenous. Thermal windows with shorter hair or thinner skin can be identified at the ventral abdomen, axillary space and inside of the thighs (about 20% of the skin), thus allowing to modulate heat dissipation. In contrast to sheep wool, lamoid fibres are mainly medullated. The thermal conductance of summer pelage was higher than that of the winter fleece and highest for the axillar and lower flanks. Lamoids have developed behavioural strategies to modify heat loss by adopting specific postures according to ambient conditions by closing or opening the thermal windows. Energy savings of 67% attributed to posture were calculated. SACs have shown to be able to adapt to a broad range of different climatic conditions. The specific integumental characteristics of SACs indicate that they have developed adaptation mechanisms particularly suited for cooler climates. Accordingly, hyperthermia might become a problem in hot, humid areas outside of their original habitat. Several studies showed the beneficial effect of shearing against heat stress. In particular, fertility in males exposed to heat stress may be improved by shearing. Infrared thermography reveals that in shorn animals the heat is radiated across the entire body surface and is not restricted to the thermal windows. However, shearing also changes the conditions of the protective layer, resulting in a loss of thermal conductance that may result in adverse effects when animals are kept under cold temperatures. The length of residual fibre appears to be crucial in avoiding excessive heat loss in a cold environment, as demonstrated by shearing experiments with different shearing machines. There is, therefore, potential for welfare considerations to conflict with industrial demands for fibre length or homogenous quality.

Keywords: fibre, thermoregulation, shearing, South American camelids

Implications

Fibre is of vital importance for endothermy in mammals. The impact of husbandry by humans, principally in shearing, modifies the thermoregulation capacity. This review highlights the role of hair for their thermoregulation in the fine fibre-producing South American camelids. Although fleece removal could be beneficial as preventative measure against heat stress, an adverse effect under cold conditions may arise from excessive heat loss following shearing. This impact depends on the length of residual fibre with shorter

fibres producing poorer insulation. There is, therefore, potential for welfare considerations to conflict with industrial demands for fibre length or homogenous quality.

Introduction

Hair fibre, synthesised from follicles located on the external integumental surface of the body (Galbraith, 2010a), is commonly regarded as a unique mammalian feature. It is assumed that mammalian hair evolved about 200 million years ago (Ruben, 1995; Meng and Wyss, 1997; Grigg *et al.*, 2004). The recent identification of reptilian genes

[†] E-mail: mgerken@gwdg.de

encoding hair keratin-like proteins revealed a new insight into the evolutionary origin of hair (Eckhart *et al.*, 2008).

Several functions have been attributed to hair fibre including barrier to cutaneous water loss, mechanical protection against abrasion of the skin, camouflage or display through hair pigmentation and an important role for endothermy (Grigg *et al.*, 2004). Hair fibre in mammals has some apparent advantages for thermoregulation over scales as found in ectotherm reptiles as it allows a more flexible adaptation of the body surface to environmental conditions. In particular, air with its minimal thermal conductivity is trapped within (medullation) and between hairs resulting in improved insulation.

In the process of domestication by humans, some species have been selected for their hair characteristics. Usually, commercialised animal fibres are divided according to their origin into wool (sheep) and fine fibre (e.g. goats, camels, South American camelids (SACs) and yak). The artificial selection resulted in marked changes with regard to follicle number, type, distribution, growth and even natural shedding (Allain and Renieri, 2010; Antonini, 2010; Galbraith, 2010a). The impact of these genetic manipulations on the adaptation and acclimatisation of the animals is not completely understood. This review focuses on the fine fibre-producing SACs and the role of hair for their thermoregulation. Emphasis will be on the relationship between integumental characteristics and thermoregulation.

Temperature regulation

The energy budget for an animal with fur depends on many factors, and several general models have been proposed

including the special role of the hair coat (e.g. Walsberg *et al.*, 1978; Turnpenney *et al.*, 2000).

Thermoregulation is part of a homeostatic mechanism related to energy metabolism as it keeps the organism at optimum operating temperature within certain boundaries, even when the surrounding temperature is very different. In mammals, endothermic homeothermy generally results from a combination of high resting, aerobically supported heat production rates (about five- to tenfold that of reptiles) in all soft tissues and sufficient insulation to retard excessive heat loss (Ruben, 1995; Grigg *et al.*, 2004).

A schematic overview on thermoregulatory mechanisms including the role of fibre is given in Figure 1. These mechanisms can be divided into those concerned with the modulation of the rate of heat production and those modulating the rate of heat flow into or out of the organism (Bligh, 1998). The processes of energy transfer include the sensible heat transfer (flow of energy into or out of the organism by convection, conduction or radiation) and the insensible heat transfer through evaporation (energy transfer from the organism to the environment). During evaporation, a thermal gradient through the peripheral body tissues from the core to the skin is created or enhanced. Evaporative cooling involves the transfer of water to water vapour, which requires 2443 J/g of water converted. The rate of sensible heat transfer through a thermal gradient depends on the magnitude of the gradient, the thermal conductivity of the intervening masses and the size of the area over which the heat transfer occurs. The evolution of subcutaneous (layer of fatty tissue) or supercutaneous (hair or feathers) thermal insulation influences the flow of heat down the thermal gradient from the organism to

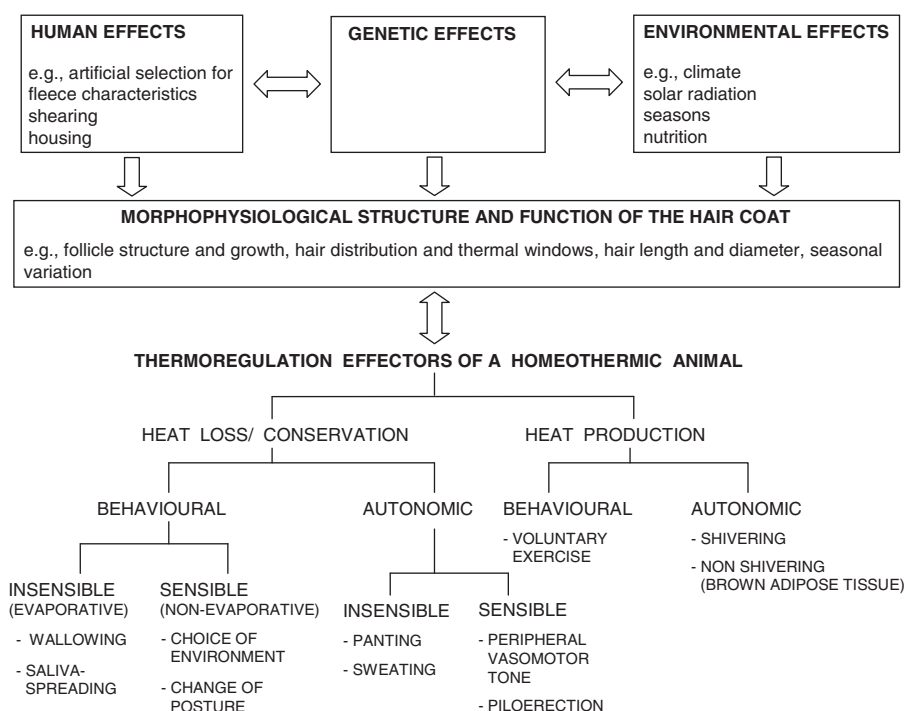


Figure 1 Schematic overview on effects acting on thermoregulatory mechanisms in a homeothermic animal including the particular role of the haircoat (modified after Bligh (1998)).

the environment (Walsberg *et al.*, 1978; de Lamo, 1990; Schmidt-Nielsen, 1997; Bligh, 1998; Jessen, 2001).

The capacity for piloerection by muscles at the base of the hairs allows the variation of the supracutaneous insulation provided by still air trapped in the hair coat, thus changing the area of the hairs relative to the skin (Bligh, 1998), comparable to feathers in birds (Gerken *et al.*, 2006).

Specific integumental characteristics in SACs related to thermoregulation

SACs originate from habitats with temperature extremes ranging from about -10°C to 30°C . The wild lamoids vicuña (*Vicugna vicugna*) and guanaco (*Lama guanicoe*) survive in a broad range of different harsh climatic conditions ranging from the Puna highlands of the Andes and altitudes above 3500 m to the sea coast. The domestic lamoids, llama (*Lama glama*) and alpaca (*Lama pacos*) have shown themselves to be able to adapt to very different climatic conditions all over the world.

During evolution, SACs have developed several integumental characteristics to allow adaptation to environmental changes (Atlee *et al.*, 1997; Fowler, 1998). It is notable that in wild lamoid guanaco and vicuña genotypes, the hair coat is formed by two types of hair – the coarse outer guard hairs and a finer undercoat, which is typical of the ‘double coat’ found in other undomesticated mammalian species. In contrast, variations in coat morphology are observed in the domesticated llamas (*L. glama*) and alpaca (*L. pacos*) that exhibit variably double coat and predominantly single coat, respectively. Further details of hair follicle morphology in SACs are given elsewhere (Antonini, 2010). The double coat may be hypothesised to represent a specific adaptation to the harsh environment in which longer thicker guard hair on the fleece surface may promote shedding of water and also act as a physical barrier against wind. The major outcome is, thus, the protection of the underlying finer undercoat and skin and the reduction of body heat loss.

In SACs, the distribution of the hair coat across the body is not homogenous, and several ‘thermal windows’ (Figure 2) can be identified at the ventral abdomen, axillary space and inside the thighs with fewer hair follicles, shorter hair or thinner skin (Fowler, 1994). Morrison (1966) estimated for a male guanaco the surface areas with fur of different thickness (Table 1). About 40% of the guanaco skin was covered by heavy fur, but almost 20% was nearly bare allowing to modulate heat dissipation (Morrison, 1966). Parallel differences in dermis thickness were described by Atlee *et al.* (1997) for the llama. The average dermal thickness was 3.1 mm. The thickest dermis was found for the neck with 4.6 and 5.1 mm for the dorsal and lateral aspects of the neck, respectively. Ventral areas were covered by a much thinner dermis of 2 to 3 mm.

The density of the hair varies with body region, with the thickest fibre on the back and the sides, and follicles that produce the hair are oriented in a sharp oblique angle (Atlee *et al.*, 1997). It is suspected that this pattern provides



Figure 2 During natural rolling behaviour, the ‘thermal windows’ at the ventral abdomen, axillary space and inside the thighs with fewer hair follicles, shorter hair or thinner skin are clearly visible. Lamoids have developed behavioural strategies to modify heat loss by adopting specific postures according to ambient conditions and thus closing or opening the ‘thermal windows’.

Table 1 Proportions of surface areas with pelage of different thickness in a guanaco (*Lama guanicoe*; from Morrison, 1966).

	Depth of pelage (mm)	Percentage of total skin area
Nearly bare	1	19
Short hair	4	20
Medium-length hair	15	20
Long hair	30	41

insulation and protection to extreme climatic conditions. This marked angulation of the hair follicle is in contrast to sheep in which the follicles are generally orientated almost perpendicular to the skin surface (Atlee *et al.*, 1997).

Each hair follicle is associated with sebaceous glands, but in lamoids, the production of grease is low in comparison to that of sheep with percentages in raw material ranging between 0.8% and 5% in lamoids v. 10% and 25% in sheep (Dawes, 1973; Duga, 1986).

The distribution of the epitrichial sweat glands varies with body location, but the sweat gland are more complex and productive in areas of the ‘thermal windows’ (Atlee *et al.*, 1997; de Lamo *et al.*, 2001). In llamas, well-developed *Arrector pili* muscles are associated with larger hair follicles in the areas of long dense haircoat (Atlee *et al.*, 1997), whereas they are small and rudimentary in areas with short sparse haircoat (‘thermal windows’).

In contrast to sheep wool, lamoid fibres are mainly medullated (Antonini, 2010). The medulla may be continuous or interrupted, empty or filled (Phan, 1994). In coarse fibre, the medulla diameter may range between 0.25% and 0.30% of the fibre diameter. Even in the very fine fibres of vicuña, medulla size was about one-fifth of the fibre diameter. It is assumed that these specific characteristics contribute to the remarkable insulating properties of lamoid fibres. However, the influence of medullation on

absorption of water by the fibre and thus its possible impact on the thermoregulative properties of the fibre are not well-known in SACs.

The thermal conductance of winter, summer and sheared pelts of guanacos was measured by guarded hot plate technique (Bulgarella and de Lamo, 2005), with thermal conductance defined as the heat flow per unit area per unit temperature difference across the fleece (Harris *et al.*, 1985). The summer pelage had higher thermal conductance than the winter fleece (1.79 v. 1.64 $\text{W/m}^2\text{ }^\circ\text{C}$), implying that more heat will flow through a surface area of the summer fleece than that in winter fleece per unit difference in temperature. Winter and summer pelage did not differ in hair length, indicating that the better winter insulation was due to a greater hair density and not to longer fibres. It was calculated that fibres longer than 5 cm would not express significant changes in conductance. The highest mean conductance (2.68 $\text{W/m}^2\text{ }^\circ\text{C}$) was found for the axillar and lower flanks, which coincide with the 'thermal windows' (Morrison, 1966; Fowler, 1994). Mean heat loss in natural fleece was 1.74 and 2.3 $\text{W/m}^2\text{ }^\circ\text{C}$ in sheared pelage, when measured in free convection conditions (Bulgarella and de Lamo, 2005).

Acclimatisation and thermotolerance

The resting body temperature of adult llamas and alpacas ranges from 37.5°C to 38.6°C (Fowler, 1998) measured in a neutral or moderately extreme ambient temperature. Normal body temperatures of neonates may be a degree higher than that of the adults (Fowler, 1994). In guanacos, body temperatures were measured by telemetry in winter and summer under natural conditions in Argentina. Body temperatures fluctuated between 37.2°C and 39.7°C in both seasons. The diurnal temperature pattern was characterised by a sinusoidal variation with high body temperatures during the daytime and low ones after the sunset with daily fluctuations larger than 1.0°C (de Lamo, 1990). In llamas and alpacas, diurnal patterns of core body temperature were found to lag behind the diurnal ambient temperature by 6 to 8 h (Bligh *et al.*, 1975).

Data on thermoneutral zones for camelids appear to lack. Some indirect conclusions may be drawn by studies conducted on sweating. In guanacos, ambient temperatures between 20°C and 33°C were the main stimuli for activation of sweat glands. The total heat loss by evaporation calculated at ambient temperatures of 20°C and 30°C were 11.9% and 37%, respectively, of the standing basal metabolic rate (de Lamo, 1990; de Lamo *et al.*, 2001). Guanacos (de Lamo *et al.*, 2001) react with sweating at rather low temperatures from 20°C (with a maximum at 25°C), whereas llamas did not show any water loss from the skin when exposed to 20°C to 25°C (Allen and Bligh, 1969).

Rosenmann and Morrison (1963) concluded from their studies that in guanacos panting occurs under work (e.g. running) but not under heat exposure. In the study by de Lamo (1990), guanacos did not change their respiratory rate when exposed to ambient temperatures between 20°C and

30°C . Thus, respiratory water loss appears not to be an important mechanism for heat dissipation in guanacos and the main channel for water loss is evaporation by sweating (de Lamo *et al.*, 2001).

SACs have shown themselves to be able to adapt to a broad range of different climatic conditions all over the world. However, they may come under severe heat stress when living in countries with extremely hot summers; animals which die from heat have been reported, for example, from Texas (Rotter, 1991; Fowler, 1994). In a hot climate, adult lamoids may maintain a daytime core body temperature of 40°C (Fowler, 1994). Body temperatures in llamas and alpacas rarely exceed 43.3°C , and animals in severe heat stress may have temperatures of only 41.1°C to 42.2°C . Protein denaturation takes place at temperatures of 45°C to 47°C , causing irreversible defects of tissues and organs (Fowler, 1994).

Alpacas are reported to be more tolerant to heat than llamas. This may be due to the larger body size in llamas compared with alpacas (Navarre *et al.*, 2001), and thus their less favourable relation between body mass and body surface for heat dissipation.

In a study by Gerken *et al.* (2003), rectal temperatures and ambient temperatures were taken in 14 adult female, unshorn llamas (ambient temperatures between -0.4°C and 25.1°C). The fibre lengths varied between 70 and 240 mm, with an average of 125.7 mm. Spearman correlation coefficients between fibre length and rectal temperatures were not significant. The highest values were obtained for the correlation with fibre length of the shoulder ($r = 0.49$) and belly ($r = 0.28$); the lowest for neck ($r = 0.13$), back ($r = -0.14$) and thigh ($r = -0.04$). The higher correlations with shoulder and belly hair length might underline the importance of these regions for thermoregulation as thermal windows (Morrison, 1966; Fowler, 1994).

Behavioural adaptation

Behavioural modification of the hair coat aiding thermoregulation includes piloerection by small muscles at the base of primary follicles. It is open to question, however, to which extent camelids are using piloerection to minimise cold or heat stress.

Lamoids have developed behavioural strategies to modify convective heat loss by adopting specific postures according to ambient conditions. The behavioural patterns include the closing or opening of the 'thermal windows', thus decreasing heat loss through radiation and convection (Atlee *et al.*, 1997). In Guanacos de Lamo *et al.* (1998), calculated energy savings of 67% attributed to posture. When the ambient temperature (T_a) was between 0°C and 10°C , the animals decreased the area of the thermal windows to 5% to 7% of the total surface area, whereas at temperatures above 10°C , animals increased the area up to 22%. When T_a was below 0°C to 1°C , the guanacos tended to bed. In llamas, Milz (2001) observed more lying with elongated neck under high temperatures.

Different behavioural activities are used to aid in heat dissipation including seeking shade or ventilated areas, orientation to minimise radiant heat gain when lying in the sunlight or recumbency to cover the thermal windows (Fowler, 1994). Lamoids are described to readily use water for cooling (Rotter, 1991). Lamoids use dry sand, dust or bare places for rolling behaviour. Subsequent to rolling, they exhibit body shaking (Pilters, 1954). The rolling behaviour may also serve to improve the thermoregulatory properties of the pelage by removing adherent sweat, grease or dirt and aligning the fibre, comparable to dustbathing in birds (Gerken *et al.*, 2006).

Fleece surface temperature

The knowledge of the surface area of an animal is important to determine the heat loss for a particular environment. In adult guanacos (80 to 100 kg), the surface area varied from 1.68 to 1.92 m² (de Lamo, 1990).

The surface temperature of an animal can be measured by the radiated electromagnetic waves. Infrared thermography offers an excellent non-invasive tool for measuring this infrared radiation on the boundary layer of an animal (de Lamo, 1990; Gerken, 1996; Gerken *et al.*, 2006; McCafferty, 2007; Schwalm *et al.*, 2008). Figure 3 shows the thermal windows at the ventral abdomen, axillary space and inside of the thighs emitting higher infrared radiation.

Surface temperature depicts the thermal energy that flows between the outer surface of the body and the environment. In a study in guanacos kept between -11°C and 27.5°C , the mean surface temperature (thermal imaging camera, measuring infrared radiation between 2 and $14\text{ }\mu\text{m}$) decreased with decreasing ambient temperature until this reached 0°C . Below that point, mean surface temperature remained nearly constant at 6°C to 8°C . In the model proposed by de Lamo (1990), radiative heat loss was calculated to fluctuate between 58.8 W/m^2 at -11°C and 23.3 W/m^2 at 27.5°C in a 90 kg guanaco.

McArthur (1991) considered the heat exchange on the coat surface in sheep kept outdoors during night. The calculated

flux density of latent heat gained at the coat surface on the back of a sheep could exceed 30 W/m^2 . When the surface temperature cools to the dew point temperature of the air, condensation onto the hair coat will occur and the fleece may accumulate up to 0.1 kg of water during the night.

Temperature within the fleece

Analysis of heat flow through animal coats is complicated due to the involvement of several modes of heat transfer. In addition, wind may open the fleece and reduce the insulation of the hair coat (Turnpenny *et al.*, 2000).

A fleece contains air spaces with water vapour that is in equilibrium with the water either absorbed or adsorbed on the wool fibres (Gatenby *et al.*, 1983), with the latent heat of vaporisation of water having an important effect on the energy budget of the animal (Walsberg *et al.*, 1978). When the skin is covered by a heavy pelage, passive transfer of water vapour across the skin is negligible. In that case, the high humidity of the air immediately above the skin prevents significant water vapour transfer unless the fur is strongly ruffled. However, in the thermal windows, the hair is so short that both sensible and insensible water loss is possible (de Lamo *et al.*, 2001). Heat dissipation from the fleece is inhibited if the fibre coat is dirty, matted, excessively long or wet (Fowler, 1994).

Solar radiation may penetrate into the coat and the depth of penetration depends on the colour (Walsberg *et al.*, 1978; Hansen, 1990; Turnpenny *et al.*, 2000) and the density of the coat. However, the fleece does not represent a purely physical system because the microclimate next to its skin is subject to control by the animal. Llama skin has been shown to have several particular features, including a very thick dermis with marked differences between dermis layers. The dermis also contains a prominent cutaneous vascular plexuses (Atlee *et al.*, 1997), which may play a role in tissue resistance during heat exchange.

Gatenby *et al.* (1983) measured temperature and relative humidity in a sheep fleece of 7 cm thickness at different distances from the skin and found that on the surface of the



Figure 3 Infrared thermography is an excellent non-invasive tool to measure the infrared radiation on the boundary layer of the hair coat. In non-sheared animals (right side), heat dissipation is mainly restricted to the 'thermal windows' (lighter shades at the ventral abdomen, axillary space and inside of the thighs), whereas more heat is radiated across a larger surface in sheared camelids (left side). False colour pictures taken in llamas with a scanner operating in the 8 to $12\text{ }\mu\text{m}$ band of the infrared spectrum, with light shades indicating higher temperatures.

fleece the temperature closely followed the air temperature, but deeper in the fleece there was much less change. During rain, the sensible heat loss from the body is increased because the thermal insulation of the fleece is reduced as air within the fleece is displaced by water. Sheep wool has been reported to absorb a considerable amount of water (1 kg fleece is assumed to absorb 2 kg of water), with the water-absorbing capacity being modified by adherent suint and grease (Gatenby *et al.*, 1983). However, comparable studies are lacking for lamoid fibre with its much lower content of grease.

Modification of the fleece

Natural moult

SAC hair is subjected to seasonal changes, such as shedding or moult, allowing morphological adaptation to seasonal climatic changes. During moult, the hair number, diameter or growth intensity are modified (Galbraith, 2010b). While wild lamoids (guanaco, vicuña) are reported to shed annually (Fowler, 1998), adult male llamas kept under natural light and ambient conditions in Scotland have been reported as shedding only partially, with 30% to 50% of the fibres being shed over an extended period (Russel and Redden, 1994).

Artificial selection

Manipulations of the fleece may influence the adaptive function of hairs thus impairing the thermoregulation capacity of the hair. In SAC, artificial selection has produced domestic genotypes differing in hair follicle morphology (Allain and Renieri, 2010). These include the *Suri* and *Huacayo* genotypes of alpaca that differ in follicle number, the ratio of primary/secondary follicles and the occurrence of natural shedding (Antonini, 2010). There are casual reports of SAC keepers on higher delicacy of the *Suri* variety as regards growth, diseases or mortality, and it is postulated that the curly hair might have less protective properties against the harsh Andean climatic conditions.

Shearing

Heat stress. The specific integumental characteristics described for SAC indicate that they have developed adaptation mechanisms particularly suited for cooler climates. Accordingly, hyperthermia might become a problem in hot, humid areas outside of their original habitat (Fowler, 1994).

In several studies, the beneficial effect of shearing on thermoregulation against heat stress was shown. In a study by Navarre *et al.* (2001), two groups of intact male alpacas were compared when kept under summer climate in central Alabama, USA. The first group ($n = 7$) was sheared to within 2 cm of their skin, the second remained not sheared. Clinical heat stress was not evident in any animals during the study. However, significant differences between treatment groups were found in rectal temperature, sodium concentration and blood urea nitrogen suggesting that non-sheared alpacas were less heat tolerant than sheared ones.

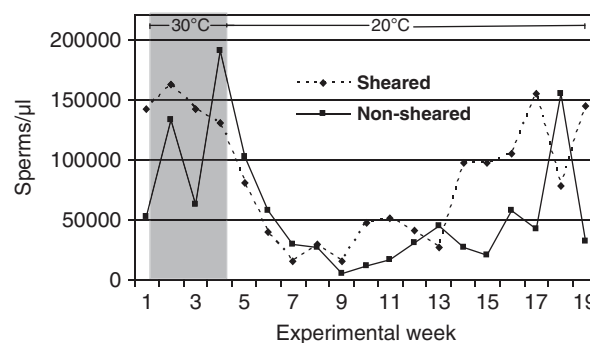


Figure 4 Spermdensity obtained from sheared ($n = 5$) and non-sheared ($n = 5$) male llamas (*Lama glama*) subjected to heat stress. During experimental weeks 1 to 4 (grey shade), animals were exposed to 30°C, followed by a recovery period at 20°C (from Schwalm *et al.*, 2008).

Similarly, Heath *et al.* (2001) exposed sheared (within 2 cm of their skin) and non-sheared male alpacas to summer climate in the United States with ambient temperatures between 22.5°C (am) and 31.5°C (pm) and relative humidity between 79.6% and 60.2%. Thermographic studies of the scrotum revealed cooler surface temperatures in sheared *v.* non-sheared animals. Temperatures of the right medial thigh of the sheared animals were 0.9°C or 1.6°C cooler than that of non-sheared animals in the morning or in the afternoon, respectively.

These results agree with the experiment by Schwalm *et al.* (2008). Ten fertile male llamas, five unshorn and five shorn, were exposed for 4 weeks to an ambient temperature of 30°C, followed by a recovery period at 20°C to study the possible beneficial influence of shearing. Parameters of thermoregulation (e.g. infrared thermography, physiological parameters) and reproduction (e.g. sperm quality and quantity) showed that heat dissipation was improved in shorn animals compared with unshorn controls. Images of infrared thermography revealed that in shorn animals the heat exchange took place over the entire body surface and was not restricted to the thermal windows only. During heat exposure, all animals were able to maintain their body temperature within the normal range. However, animals had a significantly increased respiratory rate, indicating that the adaptation of breathing rate is an important mechanism for thermoregulation in llamas. During the heat period, the sperm concentration and the sperm motility declined significantly (Figure 4).

Low environmental temperatures. Seasonal changes may be simulated by shearing and removal of fleece. Shearing may be expected to have a severe impact on thermoregulation capacity of the animal depending on age, shearing frequency, season (e.g. ambient climatic conditions), shearing technique (machine *v.* hand), and thus, the length of resulting residual hair. As shearing is an essential activity in the harvesting of fibre of SAC, it is important to be aware of the impact of the methodology used on the thermoregulation in these animals.

Shearing changes the conditions of the protective layer, resulting in a loss of thermal conductance. The mean heat loss in natural guanaco pelt was $1.74 \text{ W/m}^2\text{°C}$ compared to $2.3 \text{ W/m}^2\text{°C}$ in sheared pelage, when measured in free convection conditions. When the insulative effect of the fleece is reduced, the increased heat loss may be compensated by a higher metabolic rate (de Lamo, 1990) according to climatic conditions.

For the study of the influence of residual fibre length in llamas, different shearing machines and shearing depth were applied (Gerken and Snell, 1998). Two machines were used: a sheep shearing machine leaving a short residual fibre length of 4 to 11 mm and a more recently developed camelid shearing machine with a longer residual fibre length of 10 to 40 mm. Four adult females were shorn. The animals served as their own control with one side shorn with the sheep machine, the other side with the camelid machine. The second (control) group consisted of four unshorn adult females. Infrared thermography equipment was used for the non-invasive measurement of superficial body temperature (Thermovision® 900 System, AGEMA Infrared Systems AB, Danderyd, Sweden) with a high resolution of 0.1°C , accuracy of $\pm 0.5\text{°C}$ and temperature measurement range from -30°C to 1.500°C . A scanner operating in the 8 to $12 \mu\text{m}$ band of the infrared spectrum was used as infrared detector. Further details are provided elsewhere (Gerken, 1996). The traits recorded were residual fibre length, surface body temperature by infrared thermography and deep body temperature as measured by rectal temperature. The rectal temperature of the animals was taken at monthly intervals using a digital thermometer of 0.01°C precision. Immediately after shearing (Figure 5), the mean difference in surface temperatures between the sides

shorn by sheep or camelid machine in the same animal was about 2°C at 25°C ambient temperature. Shearing resulted in a very evenly distributed hair length of about 5.8 mm (range between 3 and 10 mm). After 6 months, the difference between both body sides was very small (Figure 6).

The recording of the rectal temperature revealed the impact of residual fibre length on core body temperature (Table 2). At lower ambient temperatures (December and January), core body temperature tended to be lower in shorn animals ($P=0.1$, one tailed Mann–Whitney U-test). However, the overall means for unshorn and shorn animals were not significantly different (37.25 ± 0.12 v. 37.13 ± 0.12 ; $P=0.25$).

It is concluded that the residual fibre length has an important role in maintaining endothermy in fine fibre-producing animals such as SAC. However, this impact largely

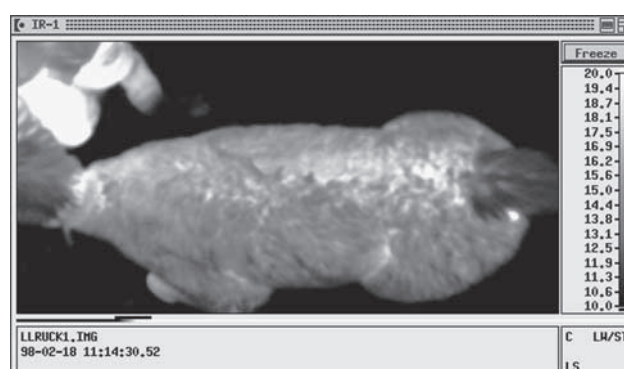


Figure 6 Superficial temperature (measured by infrared thermography with scanner operating in the 8 to $12 \mu\text{m}$ band of the infrared spectrum) for body sides in a female llama shorn with sheep machine (right body side, above) and camelid machine (left body side, below) 6 months after shearing (ambient temperature 7°C). The difference between body sides is very small due to the regrowth of the fibre.

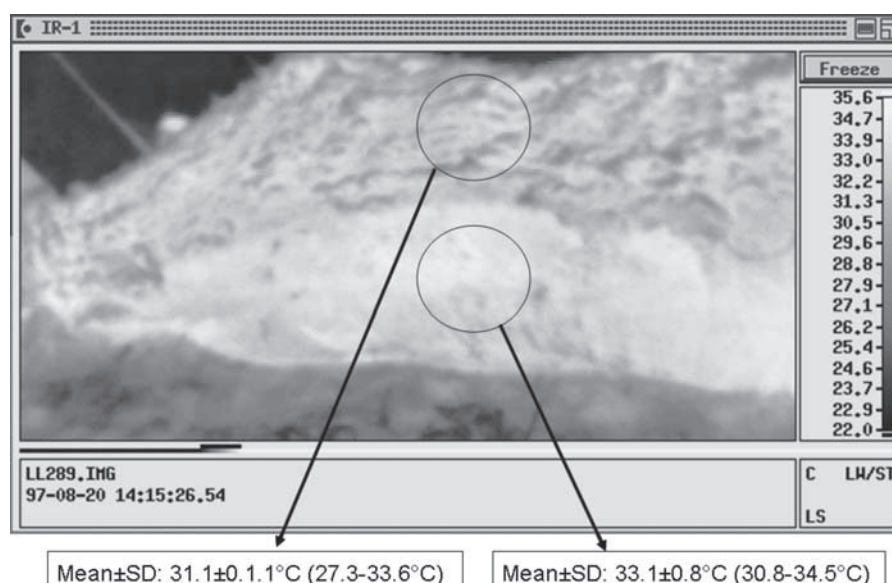


Figure 5 Superficial temperature (measured by infrared thermography with scanner operating in the 8 to $12 \mu\text{m}$ band of the infrared spectrum) for body sides in a female llama shorn with camelid machine (right body side, above) and sheep machine (left body side, below) immediately after shearing (ambient temperature 25°C). The shorter residual fibre obtained by the sheep machine results in higher surface temperatures with a difference of about 2°C between shearing machines.

Table 2 Influence of fleece length on mean rectal temperatures in adult female llamas, Germany (mean \pm s.d.; modified after Gerken and Snell, 1998)

Months	Rectal temperature (°C)			Climate	
	Unshorn (x_1) ($n = 4$)	Shorn (x_2) ($n = 4$)	Difference ($x_1 - x_2$)	Ta (C°)	Percentage of relative humidity
September 1997	37.95 \pm 0.13	37.89 \pm 0.81	0.06	12.5	48.3
October 1997	37.46 \pm 0.20	37.45 \pm 0.43	0.018	-4.5	86.5
November 1997	37.50 \pm 0.18	37.48 \pm 0.41	0.028	3.7	79.5
December 1997	37.61 \pm 0.32	37.22 \pm 0.35	0.39	-1.3	74.9
January 1998	37.40 \pm 0.40	36.83 \pm 0.47	0.57	-1.6	79.7
February 1998	37.46 \pm 0.49	37.29 \pm 0.29	0.18	6.9	76.9
March 1998	37.38 \pm 0.39	37.56 \pm 0.21	-0.18	4.5	69.7
April 1998	37.36 \pm 0.64	37.23 \pm 0.33	0.13	3.1	91.1
Overall mean	37.25 \pm 0.12	37.13 \pm 0.12	0.12		

Ta = ambient temperature.

depends on rates of regrowth of fibre. There exist genetic or species differences, as suggested by studies of Russel and Redden (1994) showing that alpacas and llamas differed in hair growth rate under European conditions.

Wild SACs

The coexistence of wild and domestic SAC species in the same habitat in its autochthonous regions of South American is probably unique. Chronicles on the Inca empire describe how populations of both vicuñas and guanacos were captured and sheared once in every 3 to 4 years (Flores Ochoa, 1994), but the ancient shearing techniques are not documented. Today, there are different approaches, for example, in Argentine, Bolivia and Peru ranging from a concept of wildness, including protection of landscape, animal welfare and genetic diversity, to breeding of vicuñas in captivity (Laker, 2006).

As outlined before, wild and domestic species differ in their hair coat morphology, moult and fibre growth that makes them probably more vulnerable to harvesting of fibres than their domestic counterparts. The long-term impacts of capture, shearing and release of wild lamoids are not well studied (Bonacic *et al.*, 2006). The harsh climate of the Altiplano may cause severe cold stress to sheared animals with insufficient protection of an insulating fleece (Eltringham and Jordan, 1981). Bulgarella and de Lamo (2005) calculated that fibres longer than 5 cm would not express significant changes in conductance for sheared guanaco pelt. However, usual sheep-shearing machines would leave residual fibre lengths of about 1 cm and less. When the insulative effect of the fleece is reduced, the increased heat loss may be compensated by a higher metabolic rate (de Lamo, 1990) according to climatic conditions. But, this compensation mechanism requires the intake of an adequate energy content in the diet, which is frequently not provided by the available native forage. In addition, climatic conditions in the Altiplano might be subject to unpredictable changes (e.g. El Niño-Southern Oscillation phenomenon).

For the further development of a conservation concept that includes the sustainable use of wildlife products from

vicuña and guanaco, the impacts of shearing techniques and the consideration of animal welfare aspects with regard to thermoregulation require further studies.

Conclusions

Fibre is of vital importance for endothermy in mammals. The impact of husbandry by humans, principally in removal of hair coat, modifies the thermoregulation capacity in SACs. Although fleece removal could have a beneficial effect on thermoregulation as preventative measure against heat stress, an adverse influence on thermoregulation under cold conditions is likely to arise from excessive heat loss following shearing. This impact is dependent on the length of residual fibre with shorter fibres producing poorer insulation and potentially conflicting with welfare of the animals, particularly in young animals (e.g. baby alpaca production) and wild SACs. In deer, more heat was lost by convection from a square metre of surface of a small animal than from a larger animal (Moen, 1973). Assuming a similar proportion in lamoids, young animals and also wild SACs might be subject to high heat loss when sheared under unfavourable climatic conditions, in particular if they cannot compensate the heat loss by increase in metabolic rate as in the case of a low energy diet (de Lamo, 1990). There is, therefore, potential for these welfare considerations to conflict with industrial demands for longer fibre length and/or homogenous quality. In the woollen process, shorter fibre of 4.5 to 5 cm is usually employed, unlike the 7 to 8 cm, which is the desired length for fibre used in the worsted operation (Patthey Salas, 1994). In SACs, the possible consequences with regard to the impairment of animal welfare are not well understood and the impact of residual fibre length for subsequent fibre regrowth and quality requires further study.

Acknowledgement

This review is based on an invited presentation at the 59th Annual Meeting of the European Association for Animal Production held in Vilnius, Lithuania during August 2008.

References

- Allain D and Renieri C 2010. Genetics of fibre production and fleece characteristics in small ruminants, Angora rabbit and South American camelids. *Animal* 4, 1472–1481.
- Allen TE and Bligh J 1969. A comparative study of the temporal pattern of cutaneous water vapor loss from some domesticated mammals with epitrichial sweat glands. *Comparative Biochemistry and Physiology* 31, 347–363.
- Antonini M 2010. Hair follicle characteristics and fibre production in South American Camelids. *Animal* 4, 1460–1471.
- Atlee BA, Stannard AA, Fowler ME, Willemse T, Ihrke PJ and Olivry T 1997. The histology of normal llama skin. *Veterinary Dermatology* 8, 165–176.
- Bligh J 1998. Mammalian homeothermy: an integrative thesis. *Journal of Thermal Biology* 23, 143–258.
- Bligh J, Baumann I, Sumar J and Pocco F 1975. Studies of body temperature patterns in South American Camelidae. *Comparative Biochemistry and Physiology A* 50, 701–708.
- Bonacic C, Feber RE and Macdonald DW 2006. Capture of the vicuña (*Vicugna vicugna*) for sustainable use: animal welfare implications. *Biological Conservation* 129, 543–550.
- Bulgarella M and de Lamo D 2005. Thermal conductance of guanaco (*Lama guanicoe*) pelage. *Journal of Thermal Biology* 30, 569–573.
- Dawes K 1973. Objective Measurement of Wool. New South Wales University Press, Sydney, Australia.
- de Lamo DA 1990. Temperature regulation and energetics of the guanaco (*Lama guanicoe*). PhD, University of Illinois, Urbana-Champaign. 184pp.
- de Lamo DA, Sanborn AF, Carrasco CD and Scott DJ 1998. Daily activity and behavioral thermoregulation of the guanaco (*Lama guanicoe*) in winter. *Canadian Journal of Zoology* 76, 1388–1393.
- de Lamo DA, Lacolla D and Heath JE 2001. Sweating in the guanaco (*Lama guanicoe*). *Journal of Thermal Biology* 26, 77–83.
- Duga L 1986. Características más importantes de las fibras provenientes de camélidos sudamericanos (llamas, alpacas y sus cruces y guanacos). Proceedings of the LANAS, Seminario Científico Regional, 1985, Montevideo, Uruguay, Editorial Hemisfero Sur, pp. 215–217.
- Eckhart L, Valle LD, Jaeger K, Ballaun C, Szabo S, Nardi A, Buchberger M, Hermann M, Alibardi L and Tschachler E 2008. Identification of reptilian genes encoding hair keratin-like proteins suggests a new scenario for the evolutionary origin of hair. *Proceedings of the National Academy of Sciences of the United States of America* 105, 18419–18423.
- Eltringham SK and Jordan W 1981. The vicuña of the Pampa Galeras National Reserve. The conservation issue. In *Problems in management of locally abundant wild animals* (ed. PA Jewell and S Holt), pp. 277–289. Academic Press, New York, USA.
- Flores Ochoa J 1994. Man's relationship with the camelids. In *Gold of the Andes: the llama, alpacas, vicuñas and guanacos of South America* (ed. J Martinez), pp. 36–286. FO Patthey and sons, Barcelona, Spain.
- Fowler ME 1994. Hyperthermia in llamas and alpacas. The veterinary clinics of North America. *Food Animal Practice* 10, 309–317.
- Fowler ME 1998. *Medicine and Surgery of South American Camelids*, 2nd edition. Iowa State University Press, Ames, IA, USA.
- Galbraith H 2010a. Fundamental hair follicle biology and fine fibre production in animals. *Animal* 4, 1490–1509.
- Galbraith H 2010b. *In vitro* methodology, hormonal and nutritional effects and fibre production in isolated ovine and caprine anagen hair follicles. *Animal* 4, 1482–1489.
- Gatenby RM, Monteith JL and Clark JA 1983. Temperature and humidity gradients in a sheep's fleece. II. The energetic significance of transients. *Agricultural Meteorology* 29, 83–101.
- Gerken M 1996. Application of infrared thermography to evaluate the influence of the fibre on body surface temperature in llamas. In *Proceedings of the 2nd European Symposium on South American Camelids* (ed. M Gerken and C Renieri), 30 August to 2 September 1995, Camerino, pp. 255–261. Università degli studi di Camerino, Camerino, Italy.
- Gerken M and Snell H 1998. Tierschutzfragen bei der Haltung von Neuweltkameliden in Europa. Proceedings of the Tagung Tierschutz und Nutztierhaltung, 5 to 7 March 1998, Nürtingen, Germany, DVG, pp. 205–211.
- Gerken M, Bramsmann S and Dörl J 2003. Evaluation of thermoregulation in llamas (*Lama glama*). Proceedings of the 3 Congreso Mundial sobre Camelidos, 15 to 18 October 2003, Potosí, Bolivia, vol. 1, pp. 135–140.
- Gerken M, Afnan R and Dörl J 2006. Adaptive behaviour in chickens in relation to thermoregulation. *Archiv für Geflügelkunde* 70, 199–207.
- Grigg GC, Beard LA and Auger ML 2004. The evolution of endothermy and its diversity in mammals and birds. *Physiological and Biochemical Zoology* 77, 982–997.
- Hansen PJ 1990. Effects of coat colour on physiological responses to solar radiation in Holsteins. *Veterinary Records* 127, 333–334.
- Harris GD, Huppi HD and Gessaman JA 1985. The thermal conductance of winter and summer pelage of *Lepus californicus*. *Journal of Thermal Biology* 10, 79–81.
- Heath AM, Navarre CB, Simpkins A, Purohit RC and Pugh DG 2001. A comparison of surface and rectal temperatures between sheared and non-sheared alpacas (*Lama pacos*). *Small Ruminant Research* 39, 19–23.
- Jessen C 2001. Temperature regulation in humans and other mammals. Springer-Verlag, Berlin, Heidelberg, New York.
- Laker J 2006. Wildlife or livestock? Divergent paths for the vicuña as priorities change in the pursuit of sustainable development. In *South American camelids research* (ed. M Gerken and C Renieri), pp. 26–27. vol. 1. Wageningen Academic Publishers, Wageningen, The Netherlands.
- McArthur AJ 1991. Thermal radiation exchange, convection and the storage of latent heat in animal coats. *Agricultural Forest Meteorology* 53, 325–336.
- McCafferty DJ 2007. The value of infrared thermography for research on mammals: previous applications and future directions. *Mammal Review* 37, 207–223.
- Meng J and Wyss AR 1997. Multituberculate and other mammal hair recovered from Palaeogene excreta. *Nature* 385, 712–714.
- Milz C 2001. Vergleichende Untersuchungen zum Verhalten von Lamas und Schafen auf der Weide. Inaugural Dissertation, Justus Liebig University Giessen.
- Moen AN 1973. *Wildlife Ecology*. WH Freeman Co, San Francisco, CA, USA.
- Morrison P 1966. Insulative flexibility in the guanaco. *Journal of Mammalogy* 47, 18–23.
- Navarre CB, Heath AM, Wenzel J, Simpkins A, Blair E, Belknap E and Pugh DG 2001. A comparison of physical examination and clinicopathologic parameters between sheared and non-sheared alpacas (*Lama pacos*). *Small Ruminant Research* 39, 11–17.
- Patthey Salas JF 1994. Textile Process for South American camelids. In *Proceedings of the European Symposium on South American Camelids* (ed. M Gerken and C Renieri), pp. 167–175. Università degli studi di Camerino, Camerino, Italy.
- Phan K-H 1994. Neue Erkenntnisse über die Morphologie von Kreatinfasern mit Hilfe der Elektronenmikroskopie. Thesis RWTH Aachen University. Verlag Mainz, Wissenschaftsverlag, Aachen.
- Pilters H 1954. Untersuchungen über angeborene Verhaltensweisen bei Tylopoden, unter besonderer Berücksichtigung der neuweltlichen Formen. *Zeitschrift für Tierpsychologie* 11, 213–303.
- Rosenmann M and Morrison P 1963. Physiological response to heat and dehydration in the guanaco. *Physiological Zoology* 36, 45–51.
- Rotter D 1991. Llamas can Beat the Heat. R&R Press, Dripping Springs, TX, USA.
- Ruben J 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Annual Review of Physiology* 57, 69–95.
- Russel AJF and Redden H 1994. Effects of season and nutrition on fibre growth in llamas. In *Proceedings European Symposium on South American Camelids* (ed. M Gerken and C Renieri), pp. 179–186. Università degli studi di Camerino, Camerino, Italy.
- Schmidt-Nielsen K 1997. *Animal Physiology*, 5th edition. Cambridge University Press, Cambridge, UK.
- Schwalm A, Erhardt G, Gerken M, Moors E and Gauly M 2008. Einfluss von Hitzebelastung auf Thermoregulation und Fruchtbarkeitsleistung bei geschorenen und ungeschorenen männlichen Lamas (*Lama glama*). *Tierärztliche Praxis* 36, 324–328.
- Turnpenny JR, McArthur AJ, Clark JA and Wathes CM 2000. Thermal balance of livestock 1. A parsimonious model. *Agricultural and Forest Meteorology* 101, 15–27.
- Walsberg GE, Campbell GS and King JR 1978. Animal coat color and radiative heat gain: a re-evaluation. *Journal of Comparative Physiology B* 126, 211–222.