

Differences in the thermal conductance of tropical and temperate bovid horns¹

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Abstract: Bovid horns consist of a highly vascularized bone core covered by a keratin sheath which seems to offer limited resistance to heat flow. Based on dynamic cooling curves measured for inverted horns filled with warm water, we developed estimates of the thermal conductance of keratin and the coefficients of convective heat transfer at the water-to-sheath and the sheath-to-air boundaries to allow us to quantify heat flux through the horn sheath. Coupled with measurements of the internal and external horn dimensions, we constructed a simplified conceptual model of sheaths from 68 horns of 14 bovid species to test the prediction that the horns of temperate bovid species offer greater resistance to heat flux than the horns of tropical bovinds. The specific heat capacity of the keratin sheath was 1.53 ± 0.07 (SD) $\text{J g}^{-1}\text{C}^{-1}$. The coefficient of conductive heat transfer for keratin was $6.30 \times 10^{-3} \pm 0.30 \times 10^{-3}$ (SD) $\text{W cm}^{-1}\text{C}^{-1}$. We estimated the coefficients of convective heat transfer at the water-to-sheath and the sheath-to-air interfaces to be $8.79 \times 10^{-3} \pm 5.20 \times 10^{-3}$ $\text{W cm}^{-2}\text{C}^{-1}$ and $2.49 \times 10^{-3} \pm 1.98 \times 10^{-3}$ $\text{W cm}^{-2}\text{C}^{-1}$, respectively. A reduction in the size of the bone core and overlying vascular bed and an increase in the thickness of the keratin sheath in temperate bovinds acted to reduce the surface area through which heat was lost to the environment. Because the surface-specific thermal conductances of temperate sheaths were lower than those of tropical sheaths, we estimate that a temperate bovid having horns of the same length and external surface as a tropical bovid would experience only 75.7% of the heat loss when facing a thermal gradient of 20°C. We argue that differences in horn morphology between temperate and tropical Bovidae appear to have evolved as adaptations to restrict heat loss in the former while facilitating heat loss in the latter group.

Keywords: thermal conductance, horns, bovidae, heat flow, cold adaptation.

Résumé: Les cornes des bovidés sont constituées d'un cornillon osseux fortement vascularisé recouvert d'un étui corné de kératine lequel semble n'offrir qu'une résistance limitée au transfert de chaleur. À partir de la dynamique des courbes de refroidissement mesurées pour des étuis cornés renversés remplis d'eau chaude, nous avons fait des estimations de la conductance thermique de la kératine et des coefficients de perte de chaleur par convection entre l'eau et les étuis cornés et entre les étuis cornés et l'air afin de nous permettre de quantifier le flux de chaleur traversant les étuis cornés. Afin de tester la prédiction que les cornes des bovidés des régions tempérées offrent une plus grande résistance au transfert de chaleur que les cornes des bovidés des régions tropicales, nous avons élaboré un modèle conceptuel simplifié des étuis cornés suivant les dimensions interne et externe mesurées sur 68 cornes de 14 espèces de bovidés. La capacité thermique spécifique de la kératine des étuis cornés était $1,53 \pm 0,07$ (SD) $\text{J g}^{-1}\text{C}^{-1}$. Le coefficient de transfert de chaleur par conduction de la kératine était $6,30 \times 10^{-3} \pm 0,30 \times 10^{-3}$ (SD) $\text{W cm}^{-1}\text{C}^{-1}$. Nous avons évalué les coefficients de perte de chaleur par convection entre l'eau et les étuis cornés et entre les étuis cornés et l'air comme étant respectivement $8,79 \times 10^{-3} \pm 5,20 \times 10^{-3}$ $\text{W cm}^{-2}\text{C}^{-1}$ et $2,49 \times 10^{-3} \pm 1,98 \times 10^{-3}$ $\text{W cm}^{-2}\text{C}^{-1}$. Une réduction dans la taille du cornillon osseux et du réseau vasculaire le recouvrant et une augmentation dans l'épaisseur de l'étui corné de kératine chez les bovidés des régions tempérées permettaient de réduire la surface par laquelle la chaleur était perdue dans l'environnement. Étant donné que les conductances thermiques par unité de surface des étuis cornés des bovidés des régions tempérées étaient plus faibles que celles des bovidés des régions tropicales, nous estimons qu'un bovidé des régions tempérées dont la longueur et la surface externe des cornes sont les mêmes qu'un bovidé des régions tropicales perdrait 75,7 % plus de chaleur lorsque soumis à un écart de température de 20 °C. Nous soutenons que les différences dans la morphologie des cornes entre les bovidés des régions tempérées et ceux des régions tropicales semblent avoir évolué comme des adaptations pour restreindre les pertes de chaleur dans le premier groupe et pour les faciliter dans le second groupe.

Mots-clés: conductance thermique, cornes, bovidae, flux de chaleur, adaptation au froid.

Introduction

Horns play a prominent role in social and sexual interactions in both temperate and tropical species of Bovidae. Because males with large horns frequently have greater access to estrus females and hence higher mating success than males with small horns, horn morphology may be

subject to strong sexual selection (Geist, 1971; Hogg, 1988) leading to the evolution of extreme sexual dimorphism in horn size, shape, and use (Eccles & Shackleton, 1986; Estes, 1991; Geist, 1966; Locati & Lovari, 1991).

Although most attention has focused on their social functions, the large horns of temperate and tropical Bovidae may represent important avenues for heat transfer. The internal bony core of bovid horns is highly vascularized, while the outer keratin sheath offers limited resistance to

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heat flow (Bubenik & Bubenik, 1990; Taylor, 1966). The exact route and rate of blood circulation through the horns is poorly understood (Taylor, 1966), but it appears that warm arterial blood arrives at the base of the horn and then circulates through the capillary bed, which is sandwiched between the bony core and the keratin sheath, before finally returning through veins located within the bone matrix (Taylor, 1962; 1966). When ambient temperature is below the temperature of the arterial blood arriving at the base of the horn, heat will be transferred across the blood-keratin boundary by forced convection, then through the keratin by conduction, and finally dissipated into the surrounding air by free or forced convection depending on wind conditions.

In hot environments, animals may use vasodilation and high arterial blood flows through the horns to unload excess heat generated by metabolic activities (Taylor, 1966). If these hot conditions persist, natural selection may favor a horn design that offers a low resistance to heat flux, facilitating the unloading of heat by conduction through the keratin sheath and convection from the horn surface.

In cold environments, however, heat conservation is likely to be of greater importance than the unloading of excess heat. Under these conditions animals may use vasoconstriction to limit the flow of blood and body heat into the horns. Because they are living tissues, the bony core and surrounding vascular tissue cannot be allowed to freeze. Thus, even if vasoconstriction is highly effective, the lowest temperature to which animals can allow the vascular bed to drop is about 0°C. In northern environments with winter temperatures of -10°C to -30°C, a horn core temperature of 0°C would still provide a considerable thermal gradient for heat loss (Picard *et al.*, 1994). Thus, in cold climates, one might expect the evolution of horn designs that offer greater resistance to heat flow, reducing heat loss and energy costs in winter when animals must survive on dormant forage of low nutritive value.

We previously demonstrated that male bovids inhabiting cold temperate climates possess at least two morphological characteristics that potentially act to reduce heat loss through the horns (Picard, Festa-Bianchet & Thomas, 1996). Compared with tropical bovids, species inhabiting cold temperate climates exhibit a reduction in the size of the bony core relative to the size of the overlying keratin sheath. A reduction in the core:sheath ratio should act to reduce the surface area of the capillary bed and hence the functional surface area through which heat is lost to the environment. The keratin sheath of temperate bovids is also thicker than that of tropical species, increasing the resistance to heat flow and reducing heat loss. Because the two morphological traits that characterize the horns of temperate bovids (a reduction in the core:sheath ratio and thickening of the keratin sheath) are found in a number of distantly related nearctic and palearctic families (Antilocapridae and Bovidae) and genera (*e.g.*, *Antilocapra*, *Bison*, *Ovibos*, *Ovis*, and *Rupicapra*), as well as in the northern, but not the southern, subspecies of *Ovis canadensis* (*O. c. canadensis* versus *O. c. mexicanus*), we previously argued that these traits were not simply phylogenetic artifacts but rather had evolved in response to varying environments (Picard, Festa-Bianchet & Thomas, 1996).

The degree to which these morphological differences affect heat flux through the horns remains unclear. Estimating heat flux based only on the external horn area of tropical and temperate bovids, Taylor (1963) concluded that temperate species did not benefit from a reduction in heat loss compared with tropical species. However, in our analysis of the morphological differences between temperate and tropical species (Picard, Festa-Bianchet & Thomas, 1996), we concluded that the relatively small area of the capillary bed and the relatively thicker overlying keratin in temperate bovids would reduce heat flow. Here, we develop a simplified conceptual model of horns to identify the primary resistances to heat flux and we use this model in a first attempt to quantify and compare heat flow in temperate and tropical bovid horns.

Material and methods

This study is based on measurements taken from 68 skulls of 14 bovid species (24 females, 40 males, and four of unidentified sex; note that in this paper we use the term bovid in a broad sense to include species in the families Bovidae, Antilocapridae, and Capridae). Because there was an insufficient number of species to allow a more fine-grained analysis, we assigned each species to one of two climatic regions based on its geographic distribution (Picard, Festa-Bianchet & Thomas, 1996). Temperate species inhabit regions where annual minima fall below 0°C, while tropical species inhabit regions where annual temperature minima remain above 0°C (Table I).

We used dynamic cooling curves to quantify heat loss from horn sheath preparations (Bakken, 1976). First, the keratin sheath was separated from the bony core and the mass of the sheath was determined. Using a thin layer of glue, two pairs of type-T thermocouples (copper-constantan, 26-gauge) were attached opposite each other on the inner and outer sheath walls, one pair located at the tip and the other pair at the base of the sheath cavity. The sheath was then inverted and filled with a known mass of water pre-heated to 50°C. The thermocouples thus registered the temperature of the inner water-to-sheath and the outer sheath-to-air interfaces. We inserted a thin stirring rod mounted on a DC motor to approximately 50% of the horn sheath length to mix the water column and prevent temperature stratification. We then secured a 2 cm thick styrofoam plate over the sheath opening to stop evaporation and ensure that heat flux passed primarily by the sheath walls. The sheath mount was surrounded by a cardboard windbreak (30 cm distance) to ensure that heat loss was primarily through free convection. The thermocouples were then connected to a 16 bit A-D converter and read at 1-3.5 second intervals for 10-40 minutes by a data acquisition programme (Datacan, Sable Systems Inc., Henderson, Nevada). We registered the cooling of the sheath and water preparation from approximately 45°C to about 25°C.

Dynamic cooling curves would not accurately measure convective heat loss if water diffused through the keratin sheath to evaporate from the outer surface. To ensure that this was not a problem, we measured evaporative water loss from the external surface of one bighorn sheep horn by

TABLE I. Species, sex, body mass, morphological measurements, and estimates of thermal conductance through the basal and distal regions of bovid horns. Note that thermal conductance, signified by R^{-1} , is expressed for the complete horn and is not surface-specific. Climatic zone refers to the geographic distribution of a species where zone 1 has annual minima below 0°C and zone 2 has annual minima above 0°C

Species	Common name	Climatic zone	Sex	Body mass ^a (Kg)	Horn length (cm)	Horn surface area (cm ²)	Core surface area (cm ²)	Basal R^{-1} (W°C ⁻¹)	Distal R^{-1} (W°C ⁻¹)	Overall R^{-1} (W°C ⁻¹)
<i>Antidorcas marsupialis</i>	Springbuck	1	?	34	28.3	216.1	127.0	0.179	0.006	0.185
<i>Antilocarpra americana</i>	Pronghorn	2	F	48	18.9	374.1	168.3	0.197	0.006	0.203
<i>Antilocarpra americana</i>	Pronghorn	2	M	53	18.3	358.0	151.0	0.172	0.007	0.179
<i>Bison bison</i>	Bison	2	F	450	26.0	317.5	256.7	0.342	0.019	0.361
<i>Bison bison</i>	Bison	2	F	450	29.2	312.0	162.1	0.223	0.007	0.230
<i>Bison bison</i>	Bison	2	F	450	23.8	213.0	123.4	0.179	0.010	0.189
<i>Bison bison</i>	Bison	2	M	800	40.1	581.6	383.9	0.411	0.022	0.433
<i>Bison bison</i>	Bison	2	M	850	49.0	782.2	506.3	0.660	0.024	0.684
<i>Bison bison</i>	Bison	2	M	918	43.2	736.0	537.2	0.594	0.029	0.623
<i>Bison bison</i>	Bison	2	M	1088	45.1	872.9	539.1	0.641	0.028	0.670
<i>Bison bison</i>	Bison	2	M	800	42.3	897.4	636.2	0.706	0.040	0.746
<i>Boselaphus tragocamelus</i>	Nilgai	1	M	270	14.0	100.7	70.8	0.093	0.007	0.100
<i>Bos grunniens</i>	Yak	2	F	799	38.9	371.5	70.8	0.170	0.004	0.174
<i>Cephalophus spp.</i>	Duiker	1	M	35	8.6	43.4	17.4	0.065	0.003	0.068
<i>Gazella thompsoni</i>	Thompson's gazelle	1	F	49	31.5	212.2	125.7	0.151	0.003	0.154
<i>Hippotragus equinus</i>	Roan antelope	1	?	225	64.1	807.9	648.3	0.788	0.013	0.801
<i>Oreamnos americanus</i>	Mountain goat	2	F	33	14.6	63.9	32.5	0.054	0.001	0.055
<i>Oreamnos americanus</i>	Mountain goat	2	F	58	21.0	105.3	42.6	0.080	0.001	0.081
<i>Oreamnos americanus</i>	Mountain goat	2	F	58	20.3	100.3	46.4	0.083	0.002	0.085
<i>Oreamnos americanus</i>	Mountain goat	2	M	60	23.0	153.8	78.7	0.170	0.005	0.175
<i>Oryx dammah</i>	Scimitar oryx	1	?	155	82.6	647.9	298.1	0.542	0.001	0.543
<i>Ovibos moschatus</i>	Muskox	2	M	305	44.0	805.5	360.3	0.514	0.005	0.519
<i>Ovis canadensis</i>	Desert bighorn	1	F	60	28.1	204.1	61.4	0.105	0.003	0.108
<i>Ovis canadensis</i>	Desert bighorn	1	M	77	57.4	721.6	237.2	0.417	0.004	0.421
<i>Ovis canadensis</i>	Desert bighorn	1	M	100	72.8	1195.7	475.0	0.667	0.009	0.676
<i>Ovis canadensis</i>	Desert bighorn	1	M	77	54.6	756.7	210.8	0.249	0.007	0.256
<i>Ovis canadensis</i>	Desert bighorn	1	M	100	80.5	1401.9	507.0	0.582	0.010	0.592
<i>Ovis canadensis</i>	Desert bighorn	1	M	100	88.9	1749.5	571.5	0.582	0.013	0.595
<i>Ovis canadensis</i>	Desert bighorn	1	M	100	78.4	1363.7	459.8	0.418	0.008	0.426
<i>Ovis canadensis</i>	Desert bighorn	1	F	65	25.1	207.3	74.9	0.069	0.002	0.071
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	65	30.2	229.7	69.9	0.146	0.003	0.149
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	58	25.3	169.5	46.3	0.083	0.002	0.085
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	60	28.1	189.9	53.6	0.065	0.002	0.067
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	60	23.6	168.9	52.7	0.066	0.004	0.070
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	55	22.7	144.0	49.2	0.083	0.003	0.086
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	65	28.4	170.5	45.8	0.049	0.002	0.051
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	68	24.7	184.5	48.9	0.097	0.003	0.100
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	65	14.9	109.1	57.8	0.055	0.004	0.059
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	52	15.2	93.2	41.9	0.068	0.006	0.074
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	55	17.6	125.8	43.7	0.066	0.005	0.071
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	F	60	18.6	138.8	50.5	0.078	0.005	0.083
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	77	61.4	861.5	326.2	0.405	0.008	0.413
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	100	70.4	1293.6	497.6	0.495	0.014	0.509
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	77	58.0	769.1	333.1	0.417	0.008	0.425
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	88	71.8	1105.0	376.0	0.473	0.009	0.482
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	100	76.0	1481.6	461.2	0.496	0.012	0.508
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	100	80.4	1375.9	456.0	0.456	0.012	0.468
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	88	51.1	804.2	367.2	0.575	0.014	0.589
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	100	75.9	1211.2	374.8	0.406	0.008	0.414
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	77	61.6	840.2	386.4	0.536	0.010	0.546
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	84	60.2	812.3	319.1	0.346	0.011	0.357
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	77	53.8	731.5	309.5	0.414	0.010	0.424
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	72	47.5	589.5	269.7	0.328	0.010	0.338
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	72	41.2	457.4	206.6	0.254	0.009	0.263
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	88	72.1	1121.4	421.5	0.428	0.008	0.436
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	30	14.4	89.1	38.5	0.073	0.010	0.083
<i>Ovis canadensis</i>	Rocky Mountain bighorn	2	M	100	81.6	1610.2	520.8	0.544	0.012	0.556
<i>Ovis dalli</i>	Dall's sheep	2	F	52	21.9	135.2	39.7	0.065	0.002	0.067
<i>Ovis dalli</i>	Dall's sheep	2	F	52	22.6	146.0	38.2	0.070	0.002	0.072
<i>Ovis dalli</i>	Dall's sheep	2	M	80	45.8	432.9	145.4	0.265	0.003	0.268
<i>Ovis dalli</i>	Dall's sheep	2	M	80	75.2	1022.2	297.1	0.325	0.004	0.329
<i>Ovis dalli</i>	Dall's sheep	2	M	80	90.8	1311.2	338.3	0.405	0.004	0.409
<i>Ovis dalli</i>	Dall's sheep	2	M	80	72.1	1198.8	471.7	0.519	0.011	0.530
<i>Ovis dalli</i>	Dall's sheep	2	M	80	86.0	1288.6	237.8	0.396	0.006	0.402
<i>Ovis dalli</i>	Dall's sheep	2	M	80	96.6	1532.5	329.7	0.411	0.003	0.414
<i>Ovis dalli</i>	Dall's sheep	2	M	80	38.8	357.7	124.3	0.191	0.006	0.197
<i>Rupicapra rupicapra</i>	Chamois	2	M	37	21.4	103.6	27.0	0.111	0.002	0.113
<i>Tragelaphus euryceros</i>	Bongo	1	?	185	67.0	992.8	850.5	1.025	0.010	1.035

^aBody masses are from museum records when available, from Festa-Bianchet *et al.* (1996), or from Nowak & Paradiso (1983).

circulating dry air over the horn surface and measuring the increase in dew-point with a chilled-mirror dew-point hygrometer. No significant elevation in dew-point was found, so we assume that evaporation was not an important route for heat loss at the horn surface.

We also measured the effect of forced convection on heat loss for a representative tropical species (a scimitar oryx, *Oryx dammah*) and a representative temperate species (a male bighorn sheep, *Ovis canadensis canadensis*) by placing the sheath-water preparation in a wind tunnel of 1.5 m²

in cross-sectional area and registering the cooling curve at windspeeds of 10, 25, and 40 km h⁻¹.

We measured the specific heat capacity of keratin (J g⁻¹°C⁻¹) by heating 50 g of keratin sheath from a Toggenburg goat (*Capra hircus*) to 100°C and plunging it into 100 g of water (5°C) held in an insulated container. The increase in water temperature for five replicate measurements, coupled with the specific heat capacity of water (4.18 J g⁻¹°C⁻¹), allowed us to estimate the specific heat capacity of keratin.

We measured the coefficient of conductive heat transfer for keratin (W cm⁻¹°C⁻¹) for one sheath of *O. canadensis* by attaching two thermocouples, one on the inner and one on the outer walls at the thickest point of the sheath. We inverted the sheath, filled it with water, and inserted a stirring rod and a small 18 W heating element. We then heated the sheath and water preparation to constant temperature while measuring internal and external surface temperatures. Calculation of the coefficient of conductive heat transfer for keratin is presented in Appendix I.

MODELING HEAT FLUX THROUGH BOVID HORNS

Two factors complicate the analysis of heat flux through bovid horn sheaths. First, because sheaths are asymmetrical structures with non-uniform dimensions, heat flux varies according to sheath region. There is thus no simple way to directly analyze heat flux in relation to size and surface area. Second, horns of tropical and temperate bovids have different morphologies which should alter the relative importance of heat flux through the basal (surrounding the central cavity and bony core) and distal regions (distal to the cavity).

To render the analysis of heat flux in relation to horn size and climatic region mathematically tractable while retaining reasonable biological accuracy, we developed a simple cylindrical model of sheaths based on morphological measurements. For each horn studied, we designed a conceptual model consisting of a solid cylinder of uniform diameter, one end of which contained an internal cylindrical cavity also of uniform diameter (Figure 1). This divided the cylindrical sheath model into two regions, a basal region surrounding the cavity and a distal region extending beyond the cavity, for which we could analyze heat flux. In these conceptual sheath models, heat could flow from the internal cavity normal to its long axis through the basal wall or parallel to the long axis through the distal wall to finally dissipate to the surrounding air.

For each sheath model, the diameter, length, and area of the cylinders were calculated from morphological measurements taken from real horns such that the ratio of the bony core to sheath surface areas and the mean wall thicknesses of the conceptual model represented those found in natural horns. We covered the sheath and the core surfaces with a fast-drying liquid plastic film, peeled the thin covering off, cut it into small flat sections, and measured surface areas with an image analyzer (Agvision, Decagon Devices, Inc., Version 1.03, Pullman, Washington). To control for absolute differences in core and sheath size, we present surface areas as core:sheath ratio. We used X-ray photographs to measure horn sheath thickness at 1-cm intervals along the

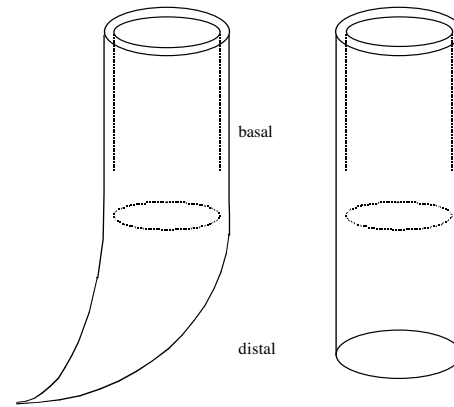


FIGURE 1. Schematic diagram of the horn and the cylindrical sheath model identifying the basal and distal horn regions.

bony core and then calculated the mean sheath thickness (cm). We measured mean diameter (cm) from diameters taken at 5 cm intervals along the sheath length. We measured the volume of the sheath cavity (cm³) with water and the volumes of the distal horn region (cm³; distal to the cavity) and of the entire sheath (cm³) by water displacement. We measured horn length as the frontal length from base to tip of the sheath. We obtained body masses from museum records, Nowak & Paradiso (1983), or from our own data on wild ungulates (Festa-Bianchet *et al.*, 1996). Table II presents the variable names and equations used to develop the conceptual models from horn measurements.

In natural horns, which we represented by cylindrical horn sheath models, heat is transported to the vascular bed overlying the bone core and then encounters three thermal resistances as it flows across the blood-keratin boundary and through the sheath to finally dissipate into the surrounding air by free convection. To calculate the three thermal resistances in our horn sheath models, we required values for the specific heat capacity of the keratin sheath, the coefficient of conductive heat transfer for keratin, and the coefficients of convective heat transfer at the water-to-sheath and the sheath-to-air interfaces. For each horn sheath, heat flux can be described by an equivalent electrical circuit formed by three resistances connected in series. The first resistance represents the convective transfer across the water-keratin boundary, the second represents the conductive transfer through the keratin matrix, and the third resistance is the convective transfer at the keratin-air boundary. Each resistance is further divided into two parallel resistances, representing resistances at the basal and distal regions. The overall thermal conductivity (R_{total}^{-1} ; W° C⁻¹) of the horn can be expressed as

$$R_{total}^{-1} = \frac{1}{\left(\frac{1}{h_1 A_p + h_1 A_{1c}} \right) + \left[\frac{1}{\frac{2\pi L_c k_k}{\ln\left(\frac{D_{ext}}{D_{int}}\right)} + \frac{k_k \left(\frac{A_{1c} + A_{2c}}{2}\right)}{L_c}} \right] + \left(\frac{1}{h_2 A_{2p} + h_2 A_{2c}} \right)} \quad [1]$$

TABLE II. Variables and equations used to design the conceptual cylindrical models for the calculation of thermal conductance and heat flux through horns

Variable	Definition	Unit	Equation
D_{ext}	mean sheath diameter	cm	
E_{mean}	mean sheath thickness	cm	
V_{cavity}	sheath cavity volume	cm ³	
$V_{extremity}$	sheath extremity volume	cm ³	
V_{sheath}	sheath volume	cm ³	
V_{total}	total sheath volume	cm ³	$V_{sheath} + V_{cavity}$
D_{int}	cavity diameter	cm	$D_{ext} - (2E_{mean})$
L_c	cavity length	cm	$(V_{total} - V_{cavity} - V_{extremity}) / \pi E_{mean} D_{ext}$
L_e	length of the extremity	cm	$4V_{extremity} / \pi D_{ext}$
A_{1p}	internal basal area	cm ²	$\pi L_c (D_{ext} - 2E_{mean})$
A_{2p}	external basal area	cm ²	$\pi D_{ext} L_c$
A_{1e}	internal distal area	cm ²	$\pi (D_{ext} - 2E_{mean})^2 / 4$
A_{2e}	external distal area	cm ²	$\pi D_{ext}^2 / 4$

where h_1 is the coefficient of convective heat transfer at the water-to-sheath interface ($W\ cm^{-2}\ ^\circ C^{-1}$), h_2 is the coefficient of convective heat transfer at the sheath-to-air interface ($W\ cm^{-2}\ ^\circ C^{-1}$), k_k is the coefficient of conductive heat transfer for keratin ($W\ cm^{-1}\ ^\circ C^{-1}$), and all other variables are as in Table II. The equations of each composite resistance that form the total horn resistance are presented in Figure 2. Linear or area measurements were made as described above. Calculations of the coefficients of heat transfer by convection at the water-to-sheath boundary and at the sheath-to-air boundary required to solve this equation are presented in Appendix II.

Within the temperature limits studied here, heat loss (Q ; W) can be predicted by $Q = R_{total}^{-1} (T_{in} - T_{out})$, where T_{in} and T_{out} are the temperatures of the inner and outer sheath surfaces, respectively.

STATISTICAL ANALYSES

Because the horns that we used in this study were not the same as those used in our previous morphological analysis (Picard, Festa-Bianchet & Thomas, 1996), we verified that the same morphological differences existed between the horns of tropical and temperate species. Before statistical analysis, we transformed the variables as required to obtain normal distributions. We performed general linear regression analysis using the square root of the core:sheath ratio as a dependant variable, log body mass and horn length as covariates, and climatic region as a categorical factor. We also performed general linear regression analysis using the square root of sheath thickness as a dependant variable, horn length as a covariate, and climatic region as a categorical factor. We did not perform phylogenetically independent contrasts on our data for two reasons. First, the purpose

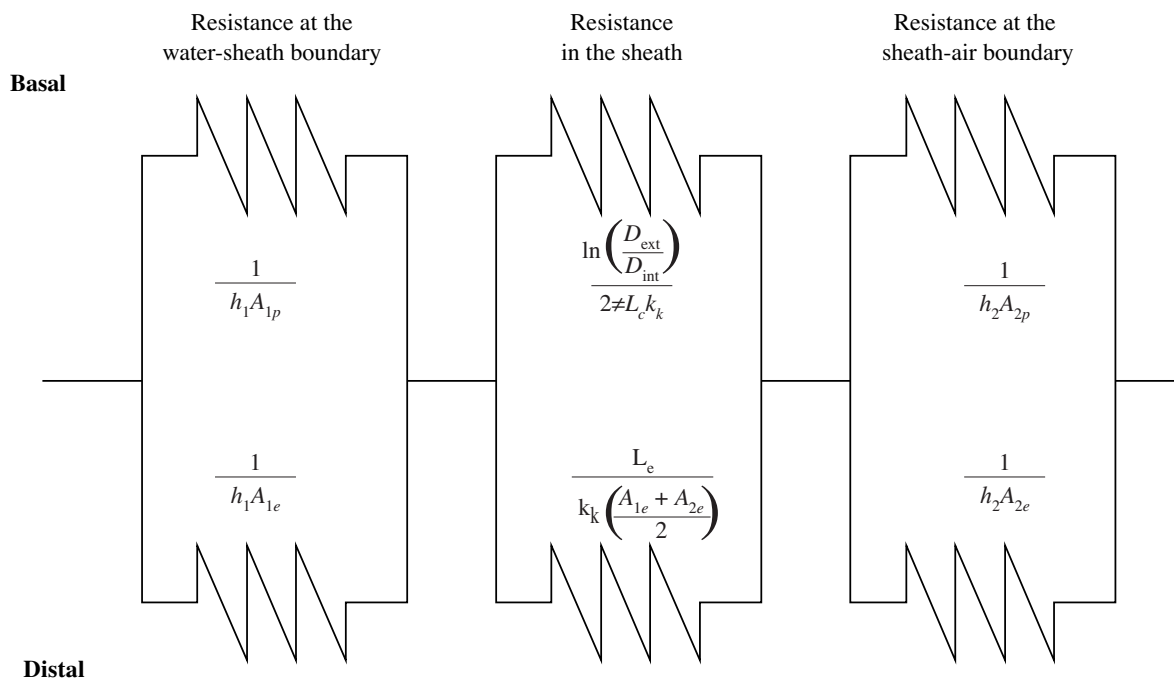


FIGURE 2. Equations for the three resistances that, when arranged in series, form the total resistance to heat flux through horns in the basal and distal regions. See Table II and equation 1 for definitions of variables.

of this paper is not to test the effect of climate on horn morphology (for this see Picard, Festa-Bianchet & Thomas, 1996), but rather to quantify the effect of morphology on heat flux. Second, phylogenetically independent contrasts require an unambiguous phylogenetic hypothesis before they can logically be applied (Ricklefs, 1996). Relationships between genera and species within subfamilies and tribes of the Bovidae are extremely controversial (Essop, Harley & Baumgarten, 1997), rendering a phylogenetic analysis inappropriate at this time. All values presented are mean \pm SD. Sample sizes were 15 and 53 horns representing tropical and temperate species, respectively.

Results

HORN MORPHOLOGY OF TEMPERATE AND TROPICAL BOVIDS

The horns that we used in this study confirmed the pattern that we had previously described for another sample of horns and we refer readers to Picard, Festa-Bianchet & Thomas (1996) for a more detailed treatment of morphology. Briefly, core:sheath ratio was affected by body mass and horn length and temperate bovids had significantly smaller ratios than tropical species (ANCOVA: $n = 68$; body mass: $F = 64.20$, $p < 0.001$; horn length: $F = 16.96$, $p < 0.001$; climate: $F = 8.97$, $p < 0.01$). Sheath thickness was related to horn length but not body mass and temperate species had significantly thicker sheaths than did tropical species (ANCOVA: $n = 68$; length: $F = 183.92$, $p < 0.001$; climate: $F = 17.61$, $p < 0.001$).

Morphologically, this means that the horns of temperate bovids are formed by a relatively thick keratin sheath overlying a short bone core and capillary bed. In tropical species such as roan antelope (*Hippotragus equinus*) and bongo (*Tragelaphus euryceros*), the vascularized bony core extended nearly the full length ($> 80\%$) of the keratin sheath. In contrast, in temperate bovids, typified by Dall's sheep (*Ovis dalli*) and bighorn sheep, the core extended on average only $41.3\% \pm 13.8\%$ of the horn length.

Morphological differences between tropical and temperate bovid horns were retained in the cylindrical models that we used to estimate heat flux. In fact, there was a good correlation between the core:sheath ratio of the horns and the cavity:external surface ratio of the cylindrical models ($r = 0.74$, $df = 68$, $p < 0.001$).

RESISTANCES AND THERMAL CONDUCTANCE OF HORNS

The specific heat capacity of the keratin sheath was $1.53 \pm 0.07 \text{ J g}^{-1}\text{°C}^{-1}$. The coefficient of conductive heat transfer for keratin was $6.30 \times 10^{-3} \pm 0.30 \times 10^{-3} \text{ W cm}^{-1}\text{°C}^{-1}$. We estimated the coefficients of convective heat transfer at the water-to-sheath and the sheath-to-air interfaces to be $8.79 \times 10^{-3} \pm 5.20 \times 10^{-3} \text{ W cm}^{-2}\text{°C}^{-1}$ and $2.49 \times 10^{-3} \pm 1.98 \times 10^{-3} \text{ W cm}^{-2}\text{°C}^{-1}$, respectively.

Free convection at the sheath-to-air boundary offers the single largest resistance to heat transfer, representing $47.4\% \pm 12.4\%$ and $52.4\% \pm 15.2\%$, respectively, of the overall thermal resistance for temperate and tropical horns (Figure 3). Climate did not affect the proportional contribution of the three resistances to the total thermal resistance

($F = 0.00$, $df = 1$, $p = 1.00$), but it did have an important effect on the absolute size of the resistance to heat flow. Surface-specific thermal conductance through external surface of the horn ($\text{W}^\circ\text{C}^{-1} \text{ cm}^{-2}$) was negatively correlated with horn length ($r = -0.54$, $df = 66$, $p < 0.001$), but temperate horn sheaths had significantly lower surface-specific conductances than did tropical horn sheaths (ANCOVA: $n = 68$; horn length, $F = 32.92$, $p < 0.001$; climate, $F = 6.74$, $p = 0.01$; Figure 4a). This difference was due principally to differences in the surface-specific thermal conductance at the blood-to-sheath boundary and within the keratin sheath. When expressed relative to the external horn surface, temperate bovids had a significantly lower thermal conductance at the blood-sheath boundary (ANCOVA: $n = 68$; climate, $F = 5.11$, $p = 0.03$; horn length, $F = 39.90$, $p < 0.001$; Figure 4b). Temperate bovids also had significantly lower surface-specific thermal conductance within the keratin sheath compared with tropical bovids (ANCOVA: $n = 68$; horn length, $F = 22.83$, $p < 0.001$; climate, $F = 11.59$, $p = 0.001$; Figure 4c). However, while surface-specific thermal conductance at the sheath-to-air boundary was significantly affected by horn length ($r = 0.58$, $df = 66$, $p < 0.001$), climate did not affect this relationship (ANCOVA: $n = 68$; horn length, $F = 19.57$, $p < 0.001$; climate, $F = 1.42$, $p = 0.24$). It is noteworthy that the basal horn region overlying the bone core and vascular bed contributed on average $98.2\% \pm 1.4\%$ of the thermal conductance of horns of temperate and tropical bovids.

Under forced convection, the surface-specific conductance of the temperate bighorn sheep horn ($Y = 0.385 \text{ windspeed}^{0.143}$; $r^2 = 0.93$, $n = 4$) appeared substantially lower than that of tropical scimitar oryx ($Y = 1.068 \text{ windspeed}^{0.118}$; $r^2 = 0.69$, $n = 4$; Figure 5). However, the sample size precludes statistical analysis.

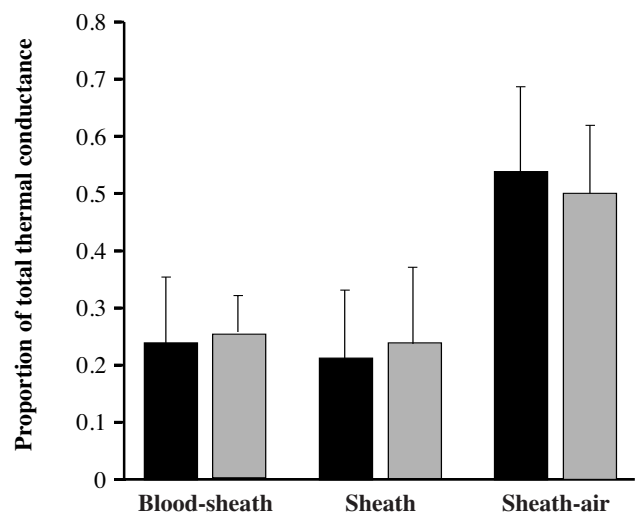


FIGURE 3. Proportion of the total resistance to heat flux contributed by convective heat transfer at the blood-sheath boundary (blood-sheath), conduction within the sheath (sheath), and convection at the sheath-air boundary (sheath-air). Black and grey histograms refer to bovids from tropic and temperate regions, respectively.

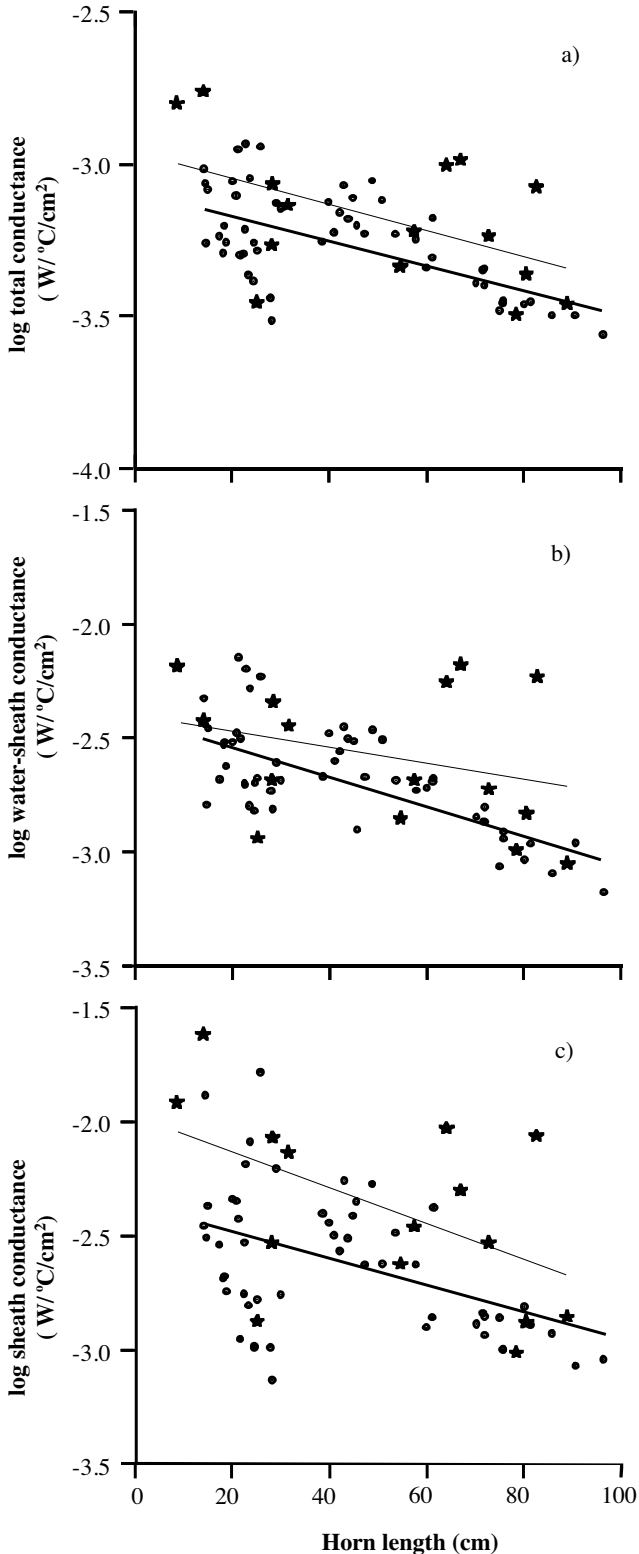


FIGURE 4. Surface-specific thermal conductances for entire horns (a), at the water-sheath boundary (b), and within the keratin sheath (c). Thermal conductances are expressed per unit area of the external horn surface and transformed as \log_{10} values ($W^\circ C^{-1} cm^{-2}$). Stars and upper thin line and circles and lower thick lines refer to tropical and temperate bovids, respectively. Least square regression lines were fitted after significant differences between tropical and temperate bovids were detected using ANCOVA (see results).

Discussion

This study confirms our previous conclusion (Picard, Festa-Bianchet & Thomas, 1996) that temperate and tropical bovids exhibit divergent horn morphologies. Tropical species support the keratin sheath on a bone core and vascular bed that extends virtually the entire length of the horn and so offers nearly the largest possible surface area for heat exchange. In contrast, temperate species exhibit a reduction in the length and surface area of the bone core and vascular bed and an increase in the thickness of the overlying sheath.

Our analysis shows that the basal sheath region, overlying the bone core and vascular bed, accounted for over 98% of the total heat flux that is dissipated from the horn sheath. This means that the reduction of the length of the bone and the consequent reduction in the surface area of the vascular bed acted to reduce the horn area involved in heat exchange, independently of the overall horn length. Temperate species not only had a smaller vascular area from which heat flows to the surface, but their thicker keratin sheath also offered a greater resistance to heat flux. Thus, under conditions of still air where heat is lost to the surrounding air primarily through free-convection, temperate species will experience lower heat loss for a given horn size at a given temperature than will tropical species.

Because most of the horn specimens were loaned by museums, we were unable to perform destructive measurements. Thus, our calculations of thermal conductance through the keratin sheath and the thermal capacity of keratin are each based on measures made on a single species (*O. canadensis* and Toggernberg goats, respectively). These values may be subject to some variation which we could not quantify. However, it was our unquantified impression that the density of the keratin sheath varied little between species, so we do not anticipate sizeable errors in our estimates.

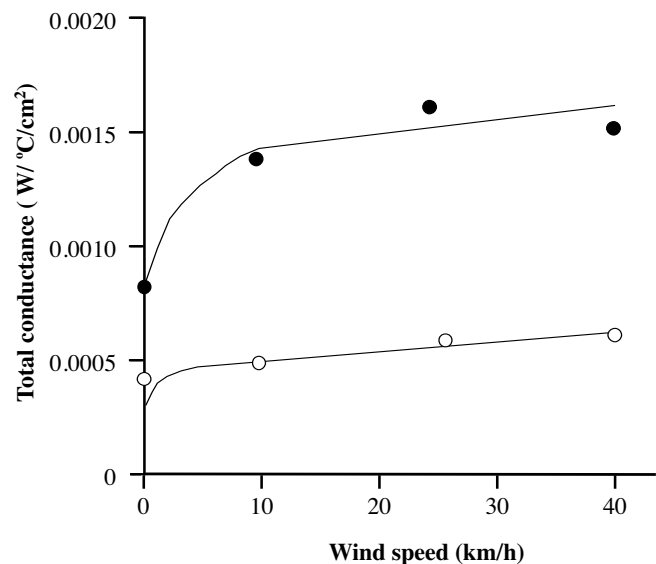


FIGURE 5. Effect of wind on the surface-specific thermal conductance of horns of bighorn sheep (*Ovis canadensis*; lower curve, empty circles) and scimitar oryx (*Oryx dammah*, upper curve, filled circles).

We can use a specific example to quantify the effect of differing horn morphology on heat flux. A tropical bovid, such as a male Barbary sheep having 80 cm long horns with an external surface of 650 cm² and facing a 20°C thermal gradient, will experience heat loss in the order of 14.0 W. In contrast, a temperate bovid, such as a Rocky Mountain bighorn sheep, possessing horns of the same external dimensions would face a heat loss of only 10.6 W, a value only 75.7% as high. This difference in heat loss is not trivial in the context of cold winter conditions and a food supply of limited quality and quantity. We previously estimated that heat flux through the horns of a male Barbary sheep would represent approximately 29% of its basal metabolic cost on a typical north-temperate winter day (Picard *et al.*, 1994).

Using heat-flow disks to measure heat loss from vasodilated horns of Toggenberg goats, Taylor (1966) estimated heat flux as 0.57 mW cm⁻²C⁻¹ in still air (see Picard *et al.*, [1994] for calculations). This amounts to 7.4 W for the above-mentioned 80 cm horn in a thermal gradient of 20°C. The difference between our modelled and Taylor's (1966) empirical estimates, which we consider slight in absolute terms (only 6.6 W difference per horn) given the drastically different methodologies, may stem from two sources. On one hand, it is difficult to ensure an adequate thermal contact between heat-flow disks and the horn due to the curved and irregular horn surface. Under this circumstance heat flux would be underestimated. On the other hand, thorough mixing of water in our horn preparations did not allow the establishment of a thermal gradient between the base of the horn where arterial blood is delivered and the distal tip. Under this condition, it could be argued that we overestimated the average internal horn temperature and hence heat flux through the sheath. However, using temperature-sensitive radio transmitters to measure surface temperatures of Barbary sheep horns, we previously showed (Picard *et al.*, 1994) that surface temperatures remain 10°C to 20°C above ambient temperature along the length of the basal horn region depending on position and ambient temperature. This indicates that Barbary sheep are unable to completely depress surface temperatures in the basal region overlying the capillary bed and so cannot substantially restrict heat loss. Thus, our estimates of heat flux based on a 20°C gradient between surface and ambient temperatures are realistic. The general agreement between Taylor's (1966) and our estimates of heat flux, along with the noted difference in size of the vascularized bone core, indicate that temperate and tropical bovid species will face very different thermal constraints under cold climates.

Under conditions where heat loss is dominated by forced convection, the differences between temperate and tropical species may be even greater. Under forced convection, thermal conductance was substantially greater for the tropical scimitar oryx than it was for the temperate bighorn sheep and this conforms with the pattern found by Wathen, Mitchell & Porter (1974), studying heat loss from metal casts of extremities. Under natural conditions, the vertical position of tropical horns, such as is found in the scimitar oryx, roan antelope, and bongo, will act to enhance the high heat loss found in forced convection. Positioned vertically on the head, horns are lifted above the low-velocity air

boundary overlying the vegetation into the higher wind-speeds. Thus, tropical species can more easily exploit the conditions favoring the unloading of excess heat generated by vigorous muscular activity such as running. In contrast, the lower, prostrate position found in temperate species, where the horns are often curled tightly beside the head or neck (*e.g.*, bighorn sheep, Dall's sheep) should act to reduce windspeed and increase the thickness and temperature of the warm boundary layer trapped at the horn surface, thus reducing convective losses.

The erect *versus* prostrate orientation of tropical and temperate horns, respectively, will also affect radiative heat gain at high solar angles, particularly in low latitude tropical regions. At mid-day when ambient temperatures are highest, the erect horns of tropical bovids will intercept less solar radiation, thus limiting heat gain while maximizing heat loss. In contrast, the prostrate orientation of temperate horns presents a larger surface area to incident radiation (although solar angles are much lower in winter at high latitudes) and thus should offer a thermal benefit to temperate bovids in northern climes.

The advantages of differing thermal conductances found in tropical and temperate bovid horns seem clear. Due to the large surface area of the vascular bed and their relatively thin keratin sheath, tropical bovids will be able to rapidly unload the excess heat generated through strenuous activity. The vertical orientation of the horns of tropical bovids places them in the region of highest air flow and so further enhances heat unloading, particularly during strenuous high-speed escapes from predators. By increasing the ability to unload excess heat, the horn morphology found in tropical bovids may allow them to limit cranial hyperthermia and so increase running stamina.

Temperate bovids, however, face a problem of heat conservation rather than heat unloading during the cold winter months when ambient temperatures may drop below -30°C and high winds increase convective heat losses. The reduced size of the vascular bed, relatively thick keratin sheath and prostrate or curled position of temperate horns act to reduce heat loss. We expect that this reduction in thermal conductance is an extremely important adaptation reducing energy requirements of temperate bovids at a time when they are forced to compete for a limited supply of low quality food.

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Appendix I

CALCULATIONS OF THE COEFFICIENT OF HEAT TRANSFER BY CONDUCTION OF KERATIN

The general equation of heat transfer by conduction through a cylinder (Q_k) is

$$Q_k = \frac{2\pi Lk}{\ln\left(\frac{r_{\text{ext}}}{r_{\text{int}}}\right)} (T_{\text{hot}} - T_{\text{cold}})$$

where L is the length of the cylinder (cm), k is the coefficient of heat transfer by conduction ($\text{W cm}^{-1}\text{C}^{-1}$), r_{ext} is the external radius of the cylinder (cm), r_{int} is the internal radius of the cylinder (cm), T_{hot} is the temperature ($^{\circ}\text{C}$) of the hottest side of the material, and T_{cold} is the temperature of the coldest side of the material (Kreith, 1993). The coefficient of heat transfer by conduction for keratin (k_k) can be calculated by isolating k and by replacing the other variables with the values developed for our conceptual horn models. The coefficient of heat transfer by conduction for keratin is thus:

$$k_k = \frac{Q_e \ln\left(\frac{D_{\text{ext}}}{D_{\text{int}}}\right)}{2\pi L_c (T_{\text{int}} - T_{\text{ext}})}$$

where D_{ext} and D_{int} are the external and internal diameters (cm), respectively, of the horn models, L_c is the length (cm) of the internal horn cavity, Q_e is the heat generated by the heating element (W), and T_{int} and T_{ext} are the temperatures of the internal and external surfaces of the sheath.

Appendix II

CALCULATIONS OF THE COEFFICIENTS OF CONVECTIVE HEAT TRANSFER AT THE WATER-TO-SHEATH AND THE SHEATH-TO-AIR BOUNDARIES

In this study, we used dynamic cooling curves to quantify heat loss from horn sheath preparations. Because these preparations are heterogeneous in structure (being formed of water and keratin) and have two boundaries (water-to-sheath and sheath-to-air), we had to derive an estimate for the coefficients of convective heat transfer at each of these boundaries.

Water contained inside the inverted horn sheath cooled at a rate determined by the temperature gradient between the water and the external environment and a cooling constant whose value depends on the thermal conductance of the sheath material (Gates, 1980). Thus, the cooling curve can be represented by

$$\frac{dT_{\text{in}}}{dt} = -p (T_{\text{in}} - T_{\text{out}})$$

where T_{in} and T_{out} are the temperatures of the water and the surrounding air, respectively, and p is the cooling constant ($^{\circ}\text{C}^{\circ}\text{C}^{-1} \text{s}^{-1}$). This expression may be integrated over time (t) to give the familiar equation for exponential cooling

$$T_{\text{in}(t)} - T_{\text{out}} = (T_{\text{in}(0)} - T_{\text{out}}) e^{-pt}$$

where $T_{\text{in}(0)}$ and $T_{\text{in}(t)}$ are the temperatures ($^{\circ}\text{C}$) of the water at time 0 and time t , respectively. Because T_{in} and T_{out} were recorded continuously during cooling trials, the cooling con-

stant may be estimated as the slope of the regression of the function

$$\ln\left[\frac{(T_{\text{in}(t)} - T_{\text{out}})}{(T_{\text{in}(0)} - T_{\text{out}})}\right] \text{ against } t.$$

In the same manner, the keratin matrix of the horn sheath cooled at a rate proportional to the difference between its mean temperature (T_{sheath} ; calculated from the mean of the internal and external wall temperatures) and the surrounding air, and to a second cooling constant whose value depends on the conductance of the sheath (Gates, 1980). Thus,

$$\frac{dT_{\text{sheath}}}{dt} = -n(T_{\text{sheath}} - T_{\text{out}})$$

where T_{sheath} is the mean temperature of the keratin sheath and n is the cooling constant ($^{\circ}\text{C}^{\circ}\text{C}^{-1} \text{s}^{-1}$). This expression may be integrated over time to give the familiar equation for exponential cooling;

$$T_{\text{sheath}(t)} - T_{\text{out}} = (T_{\text{sheath}(0)} - T_{\text{out}}) e^{-nt}$$

where $T_{\text{sheath}(0)}$ and $T_{\text{sheath}(t)}$ are the sheath temperatures at time 0 and time t , respectively. Again, because T_{in} and T_{out} were recorded continuously during cooling trials, the cooling constant may be estimated as the slope of the regression of the function

$$\ln\left[\frac{(T_{\text{sheath}(t)} - T_{\text{out}})}{(T_{\text{sheath}(0)} - T_{\text{out}})}\right] \text{ against } t.$$

Calculations of the coefficients of convective heat transfer at the water-to-sheath boundary (h_1) and the sheath-to-air boundary (h_2) were based on the basic thermodynamic equations for a well-stirred fluid (water) in a recipient (the sheath). Heat loss from the water over time (left side of the equation) is described by

$$-(c_{\text{p water}} m_{\text{water}}) \frac{dT_{\text{in}}}{dt} = h_1 (A_{1p} + A_{1e}) (T_{\text{in}} - T_{\text{sheath}})$$

where A_{1p} and A_{1e} are the internal surface areas (cm^2) of the basal and distal regions of the horn model, respectively, $c_{\text{p water}}$ is the specific heat capacity of water ($4.18 \text{ J g}^{-1}\text{C}^{-1}$), h_1 is the coefficient of convective heat transfer ($\text{W cm}^{-2}\text{C}^{-1}$), and m_{water} is the mass of water (g).

Rearranging the equation to isolate h_1 gives

$$h_1 = -\frac{(c_{\text{p water}} m_{\text{water}}) \left(\frac{dT_{\text{in}}}{dt}\right)}{(A_{1p} + A_{1e}) (T_{\text{in}} - T_{\text{sheath}})}$$

Substitution of $-p (T_{\text{in}} - T_{\text{out}})$ for dT_{in}/dt gives

$$h_1 = p \frac{(c_{\text{p water}} m_{\text{water}}) (T_{\text{in}} - T_{\text{out}})}{(A_{1p} + A_{1e}) (T_{\text{in}} - T_{\text{sheath}})}$$

Heat loss from the keratin sheath over time (left side of the equation) is described by

$$-(c_{\text{p sheath}} m_{\text{sheath}}) \frac{dT_{\text{sheath}}}{dt} = h_2 (A_{2p} + A_{2e}) (T_{\text{sheath}} - T_{\text{out}}) - h_1 (A_{1p} + A_{1e}) (T_{\text{in}} - T_{\text{sheath}})$$

where A_{2p} and A_{2e} are the external surface areas (cm^2) of the basal and distal horn regions, respectively, $c_{\text{p sheath}}$ is the

specific heat capacity of keratin ($1.53 \text{ J g}^{-1}\text{°C}^{-1}$), h_2 is the coefficient of convective heat transfer at the sheath-to-air boundary ($\text{W cm}^{-2}\text{°C}^{-1}$), and m_{sheath} is the mass of the sheath (g). Rearranging the equation to isolate h_2 and substitution of $h_1 (A_{1p} + A_{1e}) (T_{\text{in}} - T_{\text{out}})$ with $-(c_{\text{p water}} m_{\text{water}}) dT_{\text{in}}/dt$ gives

$$h_2 = \frac{-(c_{\text{psheath}} m_{\text{sheath}}) \left(\frac{dT_{\text{sheath}}}{dt} \right) - (c_{\text{p water}} m_{\text{water}}) \left(\frac{dT_{\text{in}}}{dt} \right)}{(A_{2p} + A_{2e})(T_{\text{sheath}} - T_{\text{out}})}$$

Further substitution of $-p (T_{\text{in}} - T_{\text{out}})$ for dT_{in}/dt and $-n (T_{\text{sheath}} - T_{\text{out}})$ for dT_{sheath}/dt gives:

$$h_2 = np \frac{(c_{\text{psheath}} m_{\text{sheath}}) (c_{\text{p water}} m_{\text{water}}) (T_{\text{in}} - T_{\text{out}})}{(A_{2p} + A_{2e}) (A_{2p} + A_{2e}) (T_{\text{sheath}} - T_{\text{out}})}$$