The cost of horniness: Heat loss may counter sexual selection for large horns in temperate bovids[1]

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Abstract: While sexual selection may drive the evolution of large horns in male Bovidae, heat loss from the horn's vascularized bony core in cold winters imposes an energetic cost on large-horned males. We compared horn morphology between tropical and temperate bovids to test for evolutionary adaptations to heat loss. In temperate species, the surface area of the vascularized bony core is reduced while thickness of the outer keratin sheath is increased, limiting heat flow from horns. Within the genus *Ovis*, temperate species and subspecies have thicker keratin sheaths than desert subspecies. We argue that thermal stress affecting the morphology of horns is a selective force countering sexual selection in temperate bovids.
Keywords: Bovidae, morphology, thermoregulation.

Résumé: Tandis que la sélection sexuelle semble orienter l'évolution vers des cornes de grande taille chez les bovidés mâles, la perte de chaleur au niveau des cornes dont le centre est vascularisé imposerait un coût énergétique aux animaux vivant dans des environnements froids. Nous avons comparé la morphologie des cornes de bovidés en provenance de régions tropicales et de régions tempérées pour tenter de déterminer si les animaux des régions tempérées ont développé des adaptations particulières limitant la perte de chaleur. Les bovidés mâles des régions tempérées ont des cornillons osseux moins volumineux et des étuis cornés plus épais en comparaison à ceux des régions tropicales, ce qui réduit le flux de chaleur depuis les cornes vers l'environnement. Au sein du genre *Ovis*, les espèces et les sous-espèces des régions tempérées ont des étuis cornés plus épais que les sous-espèces de milieu désertique. Le stress thermique influençant la morphologie des cornes exercerait ainsi une pression sélective contrant la sélection sexuelle chez les bovidés mâles des zones tempérées.
Mots-clés: Bovidae, morphologie, thermorégulation.

Introduction

Bovid horns play a prominent role in social and sexual interactions whereby males use their horns during combat for access to estrous females. Because males with large horns frequently have high mating success, horn morphology may be subject to strong sexual selection (Hogg, 1988; Geist, 1971) leading to the evolution of extreme sexual dimorphism in horn size, shape, and use (Estes, 1991; Locati & Lovari, 1991; Eccles & Shackleton, 1986; Geist, 1966). Indeed, the imposing horns of some male bovids are among the most striking examples of sexual selection in vertebrates.

Although most attention has focused on their social functions, horns may also be involved in thermoregulation. Bovid horns consist of a highly vascularized bony core covered by an outer keratin sheath which presumably offers limited resistance to heat flow (Bubenik & Bubenik, 1990; Taylor, 1966). Henshaw (1969), Stonehouse (1968), and Taylor (1966) all suggested that horns may offer a relatively large surface area through which excess heat can be unloaded when animals are faced with heat stress induced by hot environments. However, the same vascularization and high thermal conductivity that permit heat unloading under hot conditions may also pose an energetic load to animals living in cold temperate climates. Although Taylor (1966) showed that goats (*Capra hircus*) are able to depress horn temperatures and thus reduce heat loss to some degree, Kitchener (1991) noted that some antelope in northern zoos

suffer frostbite to their horns. As living tissue, the vascularized horn core must be maintained above freezing to avoid tissue damage and necrosis. As a result, under low ambient temperature, horns must represent a route for heat loss. We have shown that heat loss through horns amounted to the equivalent of 29% of basal metabolic rate for male Barbary sheep (*Ammotragus lervia*) when faced with temperate zone winters (Picard *et al*., 1994). However, this sub-tropical species presumably has not been subject to selection for traits reducing heat loss. Confronted with cold northern environments and hence selective pressures that differ from those encountered by tropical species, it is conceivable that temperate Bovidae evolved horn morphologies that impede heat flow from the external surface. Reducing heat flow would be particularly important when an animal is at rest and hence not generating excess heat through activity. Under these conditions, heat flow from the horns would have to be compensated by thermogenesis and so would represent an additional thermoregulatory load. This energy cost would be particularly important during winter when animals survive on dormant forage of low nutritive value (Albon & Langvatn, 1992). Thus, while the fitness benefits that accrue to males who invest in the production of large horns are clear, large horns may also impose a countering energy cost.

Heat flow from horns is affected by three major factors. The temperature of arterial blood arriving in the horn determines the thermal gradient along which heat flows to the surrounding air. Dimension of the bony core defines the

surface area of the capillary bed from which heat is lost and thickness of the keratin sheath determines the resistance to heat flow. While vasoconstriction and vasodilation provide temperate bovids with a limited ability to control heat flow to horns, only fundamental evolutionary changes in horn morphology can alter the thermal properties of horns.

We hypothesised that if large horns impose an important energetic cost on male bovids living in cold climates, then selection will act on those horn structures affecting heat loss, which will result in morphological divergence between temperate and tropical species of Bovidae. We tested two hypotheses:

1. Temperate zone bovids should have smaller ratios of core surface area to external horn area (core:sheath ratio) compared with tropical species.

2. Temperate zone bovids should have thicker keratin sheaths than tropical species.

Materials and methods

We used 54 skulls of males of 15 species to measure horn morphology. For most horns, we separated the keratin sheath from the bony core and coated each with a fast-drying plastic film. We then peeled this film off and cut it into flat pieces which were placed on an image analyser's screen. The analyser measured the total surface area of the pieces of film. When we could not separate the keratin sheath from the core, we measured core length and diameter from X-ray photographs and estimated surface area from the geometry of a symmetrical cone. To control for absolute differences in core and sheath size, we present surface areas as core:sheath ratio. We used X-rays to measure thickness of the keratin sheath at 1-cm intervals along the bone core of all specimens. We calculated mean sheath thickness as the average of the sheath thickness measurements for each horn. Body mass was from museum records or from our own data on wild ungulates (Festa-Bianchet *et al.*, 1996). Horn length was measured directly as the frontal measurement from the base to the tip of horns. We assigned species to two climatic regions. Temperate species inhabit regions where annual temperature minima fall below 0°C. Tropical species inhabit regions where annual temperature minima remain above 0°C.

Before statistical analysis, we transformed the variables as required to obtain normal distributions. We performed general linear regression analyses using log core:sheath ratio as the dependent variable, log body mass and horn length as covariates and climatic region as a categorical factor. Both log body mass and horn length significantly affect log core:sheath ratio (log body mass: $r = 0.48$, df = 52, $P = 0.0002$; horn length: $r = -0.45$, df = 52, $P = 0.0007$). To account for log body mass in our analyses, we regressed the residual variation in log core:sheath ratio on horn length using climate as a categorial factor. Square root of sheath thickness was only significantly affected by horn length ($r = 0.76$, df = 52, $P = 0.0001$) and not by the log body mass ($r = 0.16$, df = 52, $P = 0.24$), so we performed regressions on the original values again using climate as the categorical factor.

Results

The horns of tropical Bovidae differ in morphology

from those of temperate bovid species. In tropical species such as *A. lervia*, bushbuck (*Tragelaphus scriptus*), and waterbuck (*Kobus ellipsiprymnus*), the vascularized bony core extends nearly the full length of the keratin sheath. In contrast, in temperate bovids, typified by Dall's sheep (*Ovis dalli*) and Bighorn sheep (*Ovis canadensis*), the core extends on average $40.32 \pm 13.40\%$ of the length. Regression analyses confirm that climatic region significantly affects both core:sheath ratio and sheath thickness (Table I). For a given horn length, temperate species have smaller core:sheath ratios and thicker sheaths than tropical species (Figure 1). In order to overcome the potential statistical problem related to pooling a relatively large sample of *Ovis* specimens with several data points for other bovids, we carried out the same analyses including one *O. canadensis* from temperate and one from tropical climates and one *O. dalli*, all randomly chosen from our sample. Even with the reduced sample, climatic region significantly affected the core:sheath ratio ($F = 7.87$, df = 1, $P = 0.01$) and the sheath thickness ($F = 26.16$, df = 1, $P = 0.001$).

The difference in core:sheath ratio and sheath thickness between temperate and tropical bovids could be an evolutionary response to the mechanical properties required for different combat styles, rather than to selection for reduced heat loss. Most tropical bovids engage in wrestling or pushing matches, while many temperate bovids engage in powerful head butting (Kitchener, 1985; 1991). Butting generates
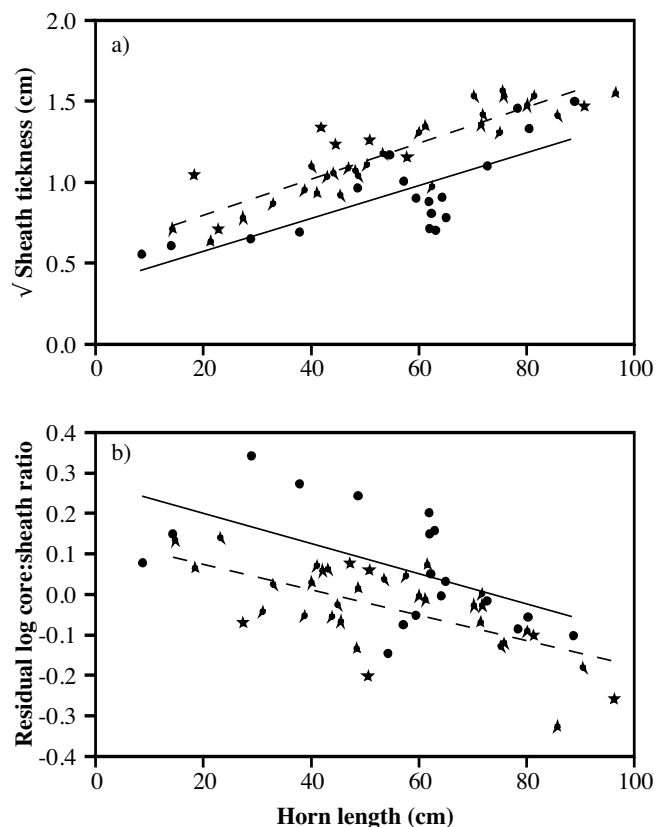

FIGURE 1. √ Horn thickness (a) and log core:sheath ratio (b; corrected for the effect of log body mass) as a function of horn length showing the effect of climate (tropical-circles; temperate-stars). The solid regression line is for tropical species while the dashed line is fitted for temperate species.

Table I. General linear regression analysis of the effect of climatic region, horn length and body mass on horn morphology. Analyses used log core:sheath ratio, log body mass, and square root of thickness

Variable	F	P
a) Core:sheath ratio ($n = 54$)		
Climate	14.18	0.0004
Body mass	32.23	0.0001
Horn length	27.24	0.0001
b) Sheath thickness ($n = 54$)		
Climate	37.38	0.0001
Horn length	128.51	0.0001

extreme shock and may demand greater external protection in the form of thick keratin sheaths.

To control for combat style, we restricted our previous analysis to 32 horns of North American *Ovis* which are distributed across both climatic regions yet use a single, head-butting combat style (Geist, 1971). As with bovids in general, climatic region significantly affects sheath thickness ($F = 4.82$, df = 1, $P = 0.037$). Male *Ovis* from temperate regions have thicker keratin sheaths than males *Ovis* from hot regions. We could not detect an effect of climatic region on core:sheath ratio in the genus *Ovis* ($F = 0.00$, df =1, $P = 0.99$). However, Wehausen & Ramey (1993), with a much larger sample size, found that for a given horn volume, desert *Ovis* had longer horn cores than northern *Ovis*.

Discussion

Our analyses show that male bovids inhabiting cold temperate climates had at least two morphological characteristics that probably reduce heat loss through the horns. Rather than a fortuitous correlation resulting from mechanical constraints imposed by different combat styles, the differences in horn morphology between temperate and tropical ungulates appear to be driven by thermal constraints. The small core:sheath ratios of temperate bovids may act to reduce the surface area of the capillary bed overlying the bony core, relative to the overall horn size. A reduction in the vascularized core decreases the functional surface area through which heat is lost to the environment. Thus, heat flow is no longer determined by the external surface area of the horn, but rather occurs through a much smaller area. The increased thickness of the keratin sheath of temperate bovids compared with tropical species may act to increase the resistance to heat flow and so should represent an enhanced insulation factor. It is interesting to note that at the generic level (genus *Ovis*), sheath thickness appears to be more responsive to selective pressure than core:sheath ratio. There might be a mechanical constraint whereby a minimum core size is required to support the relatively massive keratin sheath and the forces generated by head butting. The analyses of *Ovis* specimens were carried out to examine if the morphological characters were found within a single genus. We could not repeat these analyses with more taxa because we did not have access to a sufficient variety of bovid skulls. It would be interesting to determine the robustness of our results by repeating our analyses within taxonomic groups. Potential candidate groups are the

Rupicaprinae (*Oreamnos, Rupicapra, Capricornis* and *Nemorhaedus*) and the ibex and wild goats: both groups include species and subspecies whose range extends from hot tropical to subarctic regions.

In his analysis of horn size in relation to geographical and climatic distribution, Taylor (1966) found no simple correlation as would have been expected if thermal constraints affected horn morphology. However, he estimated heat loss from the external area of the keratin sheath and did not take into account that external horn surface and the size of the internal bony core may be subject to different selective pressures. As is generally accepted, large horn size may be the result of positive sexual selection interacting with environmental factors (Geist, 1971). The size of the bony core, however, may be subject to differing selective pressures depending on climate. Large cores and thin sheaths may be adaptive under hot tropical climates while smaller cores and thicker sheaths may be favoured under cold temperate climates.

Our results suggest that the metabolic burden of heat loss imposes a fitness cost on males endowed with large horns. Without adaptations to reduce heat loss, males with large horns would be faced with high thermoregulatory costs approaching or even exceeding 29% of basal metabolic rate as we observed in *Ammotragus lervia* held in a north temperate zoo. When food is unlimited, animals may be able to sustain this metabolic load. However, while surviving on winter forage limited in both quality and quantity, we suggest that heat loss would act as a strong force countering sexual selection for large horns. Natural selection may have acted to limit heat loss in temperate bovids by reducing the size of the bony core. However, if a role of the bony core is to support the relatively massive keratin sheath against shock, there must be a lower limit to the size of the core and hence sheath size. At this limit, selection for reduced heat loss would act to counter sexual selection for increased horn size.

Our contention that thermal constraints affect horn size and morphology is further supported by the geographic pattern of horn size in female caprids in which sexual selection presumably does not drive large horn size. Females of the desert-adapted *Ammotragus lervia*, with sheath areas approaching 500 cm^2, have much larger horn cores than females of similar-sized temperate *Ovis*, with sheath areas of only 160 cm^2. Even within the species *O. canadensis*, females of desert-dwelling subspecies have longer horn cores than females of northern subspecies (Wehausen, 1989). Differences in the use of horns for intraspecific competition could be an alternative explanation for the differences in horn size of females of *Ammotragus* and *Ovis*. However, to our knowledge, there are no data suggesting that competition for scarce resources is greater for female *Ammotragus* than for female bighorn.

It is noteworthy that antlers, which do not impose a thermal cost under cold winter conditions, are not subject to the same selective force countering sexual selection as horns. Thus, sexual selection has driven the antlers of northern cervids such as the extinct Irish Elk (*Megaloceros giganteus*), the wapiti (*Cervus elaphus*), the moose (*Alces alces*), and the caribou (*Rangifer tarandus*) to substantially more imposing dimensions than horns (Geist, 1991).

Our ongoing work on heat flow through horns aims to quantify to what degree morphological differences reduce heat flow from horns of temperate bovids compared to tropical bovids.

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APPENDIX I. Climate category and morphometric measurements of bovid skulls ($n = 54$)

Name	Scientific name	Climate	Body mass (kg)	Horn lenght (cm)	Core surface (cm^2)	Sheath surface (cm^2)	Sheath thickness (cm)
Impala	*Aepyceros melampus*	Tropical	53	63.1	279.35	536.14	0.50
Impala	*Aepyceros melampus*	Tropical	53	62.1	275.49	538.63	0.52
Hartebeest	*Alcelaphus burselaphus*	Tropical	163	59.6	104.62	678.57	0.82
Barbary sheep	*Ammotragus lervia*	Tropical	123	48.8	646.75	862.80	0.92
Pronghorn	*Antilocapra americana*	Temperate	53	18.3	150.99	358.00	1.08
Bison	*Bison bison*	Temperate	800	40.1	383.93	581.61	1.20
Bison	*Bison bison*	Temperate	850	49.0	506.27	782.20	1.08
Bison	*Bison bison*	Temperate	918	43.2	537.21	736.00	1.07
Bison	*Bison bison*	Temperate	1088	45.1	539.10	872.88	1.51
Bison	*Bison bison*	Temperate	800	42.3	636.17	897.36	1.78
Nilgai	*Boselaphus tragocamelus*	Tropical	270	14.0	70.84	100.66	0.38
Duiker	*Cephalophus* sp.	Tropical	35	8.6	17.35	43.35	0.31
Waterbuck	*Kobus ellipsiprymnus*	Tropical	175	65.1	341.33	691.62	0.62
Waterbuck	*Kobus ellipsiprymnus*	Tropical	175	64.3	405.45	886.53	0.83
Waterbuck	*Kobus ellipsiprymnus*	Tropical	175	62.4	383.28	737.49	0.66
Waterbuck	*Kobus ellipsiprymnus*	Tropical	175	62.0	544.75	745.93	0.78
Mountain goat	*Oreamnos americanus*	Temperate	60	23.0	78.71	153.78	0.50
Muskox	*Ovibos moschatus*	Temperate	305	44.0	360.27	805.51	1.10
Bighorn sheep	*Ovis canadensis*	Temperate	77	61.4	326.15	861.53	1.82
Bighorn sheep	*Ovis canadensis*	Temperate	100	70.4	497.60	1293.60	2.35
Bighorn sheep	*Ovis canadensis*	Temperate	77	58.0	333.11	769.10	1.32
Bighorn sheep	*Ovis canadensis*	Temperate	88	71.8	376.03	1104.98	1.85
Bighorn sheep	*Ovis canadensis*	Temperate	100	76.0	461.17	1481.59	2.37
Bighorn sheep	*Ovis canadensis*	Temperate	100	80.4	455.97	1375.89	2.19
Bighorn sheep	*Ovis canadensis*	Temperate	88	51.1	367.17	804.20	1.58
Bighorn sheep	*Ovis canadensis*	Temperate	100	75.9	374.83	1211.18	2.45
Bighorn sheep	*Ovis canadensis*	Temperate	77	61.6	386.42	840.15	0.94
Bighorn sheep	*Ovis canadensis*	Temperate	84	60.2	319.14	812.30	1.71
Bighorn sheep	*Ovis canadensis*	Temperate	77	53.8	309.45	731.51	1.38
Bighorn sheep	*Ovis canadensis*	Temperate	72	47.5	269.71	589.45	1.16
Bighorn sheep	*Ovis canadensis*	Temperate	72	41.2	206.60	457.37	0.87
Bighorn sheep	*Ovis canadensis*	Temperate	88	72.1	421.54	1121.44	2.00
Bighorn sheep	*Ovis canadensis*	Temperate	30	14.4	39.47	89.11	0.51
Bighorn sheep	*Ovis canadensis*	Temperate	100	81.6	520.75	1610.15	2.34
Bighorn sheep	*Ovis canadensis*	Temperate	50	33.0	110.93	294.08	0.75
Bighorn sheep	*Ovis canadensis*	Tropical	77	57.4	237.19	721.64	1.02
Bighorn sheep	*Ovis canadensis*	Tropical	100	72.8	474.97	1195.67	1.22
Bighorn sheep	*Ovis canadensis*	Tropical	77	54.6	210.79	756.68	1.37
Bighorn sheep	*Ovis canadensis*	Tropical	100	80.5	507.00	1401.88	1.78
Bighorn sheep	*Ovis canadensis*	Tropical	100	88.9	571.53	1749.45	2.26
Bighorn sheep	*Ovis canadensis*	Tropical	100	78.4	459.84	1363.69	2.14
Dall's sheep	*Ovis dalli*	Temperate	80	45.8	145.35	432.93	0.84
Dall's sheep	*Ovis dalli*	Temperate	80	75.2	297.14	1022.16	1.73
Dall's sheep	*Ovis dalli*	Temperate	80	90.8	338.25	1311.18	2.16
Dall's sheep	*Ovis dalli*	Temperate	80	72.1	471.66	1198.82	2.02
Dall's sheep	*Ovis dalli*	Temperate	80	86.0	237.76	1288.63	1.99
Dall's sheep	*Ovis dalli*	Temperate	80	96.6	329.71	1532.47	2.40
Dall's sheep	*Ovis dalli*	Temperate	80	38.8	124.31	357.70	0.90
Dall's sheep	*Ovis dalli*	Temperate	80	50.7	123.21	501.52	1.22
Dall's sheep	*Ovis dalli*	Temperate	80	48.7	148.28	514.48	1.14
Chamois	*Rupicapra rupicapra*	Temperate	37	21.4	27.02	103.55	0.40
Saiga	*Saiga tatarica*	Temperate	48	27.4	61.04	202.53	0.61
Bushbuck	*Tragelaphus scriptus*	Tropical	50	37.8	239.55	354.84	0.49
Bushbuck	*Tragelaphus scriptus*	Tropical	50	28.8	193.40	243.60	0.43