

BOVID HORNS: AN IMPORTANT SITE FOR HEAT LOSS DURING WINTER?

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Bovoid horns play a prominent role in social and sexual interactions. In cold climates, however, heat loss through the horn surface may represent a major energy cost. We measured surface temperatures of horns (T_h) for two Barbary sheep (*Ammotragus lervia*; one male and one female) at the Granby Zoo, Québec, using temperature-sensitive radiotransmitters. Over ambient temperatures (T_a) of 5 to -19°C , T_h never dropped below 3°C . At $T_a \approx -10^\circ\text{C}$, the difference between T_h and T_a was 17°C for the male and 21°C for the female. Using empirical models to predict heat loss through horns and resting metabolic rates, we estimate that, at T_a of $\approx -10^\circ\text{C}$, heat loss through the horn surface is 20% of resting metabolic rate for females and 29% for males which have larger horns than females. We argue that the metabolic costs of possessing large horns in cold climates may impose constraints on morphology and sexual selection.

Key words: horns, heat loss, energetic costs

Bovoid horns play a prominent role in social and sexual interactions, and, in most species, there is pronounced sexual dimorphism in horn size, shape, and use (Eccles and Shackleton, 1986; Estes, 1991; Geist, 1966; Locati and Lovari, 1991). Because males with large horns frequently have high mating success, horn size may be subject to strong sexual selection in males (Geist, 1971; Hogg, 1988).

The internal bony core of bovid horn is highly vascularized, while the outer keratin sheath presumably offers limited resistance to heat flow (Bubenik and Bubenik, 1990; Taylor, 1966). Considerable amounts of heat could be lost through the horn surface, particularly in large-horned species. Horns were, thus, attributed a potential thermoregulatory role as heat-dissipation structures in hot weather (Henshaw, 1969; Stonehouse, 1968; Taylor, 1966). Surprisingly, the possibility that heat loss may be a cost in winter, rather than a benefit in summer, was

hardly considered. Kitchener (1991) did note, however, that some antelope in northern zoos suffer frostbite to their horns.

Because they are living tissue, the bony core and surrounding vascular tissue cannot be allowed to freeze, and, because of the proximity of the brain, it may be necessary that horns be kept above freezing. In some large-horned, north-temperate ungulates, such as members of the subfamily Caprinae (genera *Ovis*, *Capra*, and *Ammotragus*), heat loss through the horn surface in winter may represent a sizeable metabolic load. This energy cost may be particularly important during winter when animals must survive on dormant forage of low nutritive value (Albon and Langvatn, 1992).

Here, we report on measurements of surface temperatures of horns (T_h) in captive Barbary sheep (*Ammotragus lervia*) as a first step toward the measurement of heat loss through the horns. We tested the hypothesis that animals would maintain high

T_h at ambient temperatures (T_a) below 0°C to avoid the risk of necrosis that might result from freezing of live tissue.

MATERIALS AND METHODS

We measured T_h of two adult Barbary sheep, a male (116 kg) and a female (65 kg), held as part of a herd in a 225-m² outdoor enclosure at the Granby Zoo, Québec. On 3 December 1992, we placed two pre-calibrated, temperature-sensitive radiotransmitters (Holohil Systems Inc., Woodlawn, Ontario) on one horn of each sheep. One radiotransmitter was placed 4 cm from the base, and the other half-way up the horn on the posterior surface to prevent damage during social interactions. Transmitters were attached to the horn with epoxy resin, and the tip of the 5-mm long sensor probe was inserted into a 2-mm deep hole drilled in the keratin horn sheath. The sensor and surrounding keratin were not covered by the transmitter body. Unfortunately, the transmitter in the mid-section of the male's horn malfunctioned, and we only obtained measurements of temperature from the horn base for this animal.

For each horn of the two study animals, we measured total length on the inside (male = 46.9 cm, female = 27.8 cm) and outside of the curl (male = 73.6 cm, female = 37.8 cm). We then measured the circumference at the base and at 10 cm intervals along the horn. We estimated total horn surface by assuming that horns were a series of 10-cm cylinders topped by a cone. Unlike bighorn sheep (*Ovis canadensis*) that have rather short bony cores (Geist, 1971), cones of horns of Barbary sheep reach to within <10 cm of the horn tip (C. Lanthier, pers. obser.). Therefore, in Barbary sheep, total horn surface closely estimates the surface involved in heat exchange between the horns and the environment.

We measured T_h during daylight 21 times at irregular intervals between 4 December 1992 and 19 February 1993. The mid-horn transmitter from the female ceased functioning by mid-February, and we only collected 20 measurements of temperature from that transmitter. Ambient temperature during measurements varied from 5.5 to -19°C.

We compared T_h with T_a (measured at the same time at the enclosure, 1.5 m above ground) and with ΔT ($T_h - T_a$), using non-parametric Spearman rank correlation. One extreme outlier

(T_h of 22°C when T_a was -19°C) was excluded from analyses of data for the female.

RESULTS

The female had an estimated total horn surface of 1,062 cm², while the male had an estimated horn surface of 2,971 cm². For two of the three horn positions, T_h was significantly correlated with T_a (male base: $r_s = 0.67$, $n = 21$, $P = 0.003$; female mid-horn: $r_s = 0.75$, $n = 20$, $P = 0.001$; female base: $r_s = 0.37$, $n = 20$, $P = 0.1$). However, animals never allowed T_h to drop below 3°C even when T_a fell to -19°C. As a result, ΔT increased significantly with declining T_a for two of the three horn sites (Fig. 1; male base: $r_s = -0.54$, $n = 21$, $P = 0.01$; female mid-horn: $r_s = -0.61$, $n = 20$, $P = 0.008$; female base: $r_s = -0.38$, $n = 20$, $P = 0.1$). On a typical winter day in Quebec when T_a was -9 to -11°C, mean ΔT was 17.4 (male base), 21.5 (female base), and 20.5°C (female mid-horn).

DISCUSSION

The maintenance of high T_h and the establishment of a temperature gradient of 17 to 21°C between the horn and surrounding air creates the conditions required for significant heat loss through horns. We estimated the total heat loss (watts; W) from horns of Barbary sheep from Taylor's (1966) empirical model of heat flux through horns of Toggenberg goats (*Capra hircus*). Vasodilated horns (mid-horn $T_h = 28^\circ\text{C}$ —Taylor, 1966: fig. 3) lost 16 mW/cm² in still air at T_a of 0°C and 27 mW/cm² in a light wind of 180 m/min (Taylor, 1966: fig. 5). These are losses of 0.57 mW cm⁻² °C⁻¹ in still air and 0.96 mW cm⁻² °C⁻¹ in a light wind. Our male and female study animals had horn surfaces of 2,971 cm² and 1,062 cm², respectively, and maintained ΔT of ca. 17 and 21°C, respectively, at T_a of ca. -10°C. We estimate that the male lost ca. 28.8 W in still air and 48.5 W in a light wind on an average winter day. The female lost ca. 12.7 and 21.4 W under the same conditions.

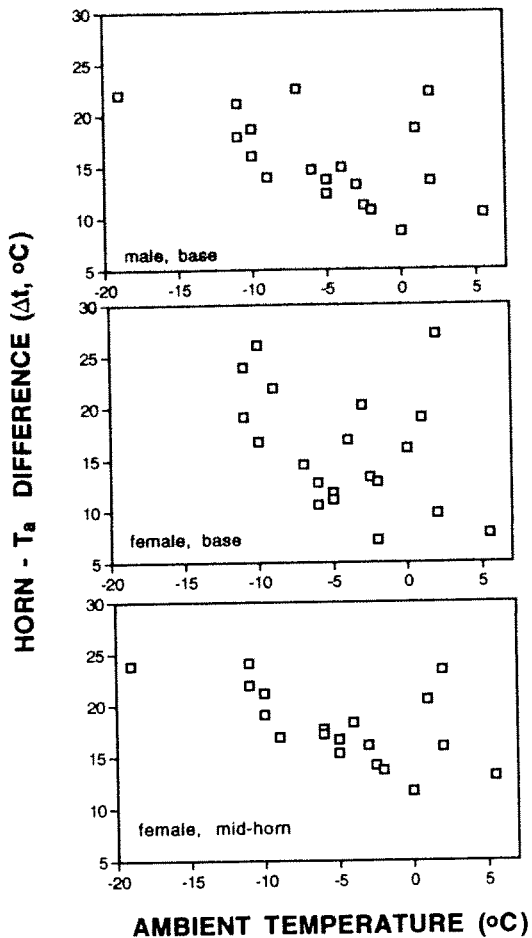


FIG. 1.—The effect of varying ambient temperature (T_a) on ΔT (the difference between horn surface and ambient temperatures) for two Barbary sheep. Temperature-sensitive radiotransmitters measured temperatures at the horn base for one male and at the base and mid-horn positions for one female.

Resting metabolic rate (in W) in the Artiodactyla scales to body mass (M in kg) as $5.21 \cdot M^{0.73}$ (Konoplev et al., 1978), so our male and female Barbary sheep would have metabolic rates in the thermoneutral zone on the order of 167.5 and 109.7 W, respectively. We estimate that heat loss through the horns amounts to ca. 29% of resting metabolic rate for adult males and 20% of resting metabolic rate for adult females on

a typical winter day with a wind of 11 km/h. If field metabolic rate (including thermoregulation and locomotory costs) is approximately three times resting metabolic rate (Nagy, 1987), the thermoregulatory load imposed by heat loss through the horns will still represent 7–10% of the total energy budget. Because animals maintain ΔT near 15°C even on warmer days ($T_a = 0$ – 5.5°C), heat loss through the horns will remain high over a wide range of T_a .

Our results have two important implications. First, if heat loss through the horns significantly affects the overall, winter, energy budget and body condition, sexual selection for greater horn size may be counterbalanced by the increasing metabolic load that they represent. Horn size in males of north-temperate species of Bovidae may be limited by the largest surface area that they can afford to sustain through the winter. Second, heat loss may partially explain subspecific and geographic variation in horn size. Females of northern bighorn sheep have smaller horns on a mass-specific basis than female southern bighorn sheep (Wehausen, 1989). Similarly, the limited available data suggest that the length of the vascularized bony horn core relative to overall horn length may be smaller for species found in cold climates (e.g., bighorn sheep) than for species inhabiting warm climates (e.g., Barbary sheep—Bubenik and Bubenik, 1990).

We studied heat loss through the horns of subtropical wild sheep kept in a northern climate; therefore, we cannot estimate how much heat is lost through the horns of cold-adapted species such as bighorn sheep, Dall sheep (*Ovis dalli*), or ibex (*Capra ibex*). However, the horns of male bighorn sheep captured in winter feel warm to the touch (M. Festa-Bianchet, pers. obser.). When these animals are exposed to temperatures below -30°C and strong winds, heat loss through the horns may be very important. Our ongoing work questions to what degree horn morphology, such as the thickness of the keratin sheath, its insulating properties,

and the relative size of the horn sheath, is shaped by seasonal heat loss.

ACKNOWLEDGMENT

This work was funded through team research grants provided to M. Festa-Bianchet from the Natural Sciences and Engineering Research Council of Canada and Fonds pour la Formation de Chercheurs et l'aide à la Recherche. This publication is no. 84 of the Groupe de recherche en écologie, nutrition et énergie.

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ACKNOWLEDGMENTS

This work was funded through individual and team research grants provided to D. W. Thomas and M. Festa-Bianchet from the Natural Sciences and Engineering Research Council of Canada and Fonds pour la Formation de Chercheurs et l'aide à la Recherche (Québec). This is publication no. 84 of the Groupe de recherche en écologie, nutrition et énergétique.

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Submitted 6 July 1993. Accepted 3 November 1993.

Associate Editor was Barbara H. Blake.

ly with a wind of 11 km/h (including thermoregulatory costs) is approximately 1.5 times resting metabolic rate. On warmer days ($T_a = 0-10^{\circ}\text{C}$), the thermoregulatory heat loss through the horns is 7–10% of the total energy loss. On colder days ($T_a = -10-20^{\circ}\text{C}$), the thermoregulatory heat loss through the horns will be 15–20% of the total energy loss. The relative size of the bony core and horn sheath, is shaped by selection against heat loss.

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