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Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep

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We used indirect calorimetry to measure energy expenditure for locomotion by three mountain goats (*Oreamnos americanus*) and five bighorn sheep (*Ovis canadensis*) in response to variation in level of activity, slope of travel, and snow conditions. The energetic increment of standing over lying averaged 26% for the two species. We could detect no difference between species in the net cost of travel on level surfaces ($\bar{x} = 0.26 \text{ mL O}_2/(\text{g} \cdot \text{km})$). Energy expended by bighorn sheep and mountain goats for lifting 1 kg of body weight one vertical metre on a 21.5° slope (ca. 37 J/(kg · m)) exceeded the highest cost documented for quadrupeds. Energy expended walking down a 21.5° slope exceeded energy expenditure for horizontal locomotion, or was recovered inefficiently (ca. 25% recovery of potential energy). The relative increase in the net cost of locomotion in snow achieved an asymptote when sinking depth exceeded 1.2–2.0 times brisket height. The slope of the relative increase in the net cost of locomotion as a function of sinking depth/brisket height was lower for mountain goats than for any North American ungulate studied to date. Consequently, mountain goats were less efficient than other species when snow was shallow, but were more efficient when it was deep. We explain this result on the basis of interspecific differences in locomotory behavior and foot loading.

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Nous avons utilisé une technique de calorimétrie indirecte pour mesurer la dépense énergétique reliée à la locomotion chez trois Chèvres de montagne (*Oreamnos americanus*) et cinq Mouflons bighorn (*Ovis canadensis*) en réaction à des variations dans l'activité, la pente du terrain parcouru et les conditions de la neige. L'augmentation énergétique reliée à la posture debout par rapport à la posture couchée était en moyenne de 26% chez les deux espèces. Le coût net de la locomotion sur les surfaces planes était le même chez les deux espèces ($\bar{x} = 0,26 \text{ mL O}_2/(\text{g} \cdot \text{km})$). L'énergie dépensée par les mouflons et les chèvres pour lever 1 kg de masse sur 1 m à la verticale sur une pente de 21,5° (ca. 37 J/(kg · m)) excédait la dépense la plus élevée jamais enregistrée chez un quadrupède. L'énergie dépensée pour descendre une pente de 21,5° excédait la dépense énergétique reliée à la locomotion horizontale ou était récupérée inefficacement (récupération d'environ 25% de l'énergie potentielle). L'augmentation relative du coût net de la locomotion dans la neige atteignait une asymptote lorsque la profondeur de l'enfoncement atteignait plus de 1,2–2,0 fois la hauteur de la poitrine. La pente de l'augmentation relative du coût net de la locomotion, calculée comme fonction de la profondeur de l'enfoncement sur la hauteur de la poitrine, était plus élevée chez les chèvres que chez tout autre ongulé nord-américain étudié. Conséquemment, les chèvres de montagne ont une locomotion moins efficace que les autres espèces quand la couche de neige est mince, mais plus efficace quand la couche de neige est épaisse. Ce résultat peut s'expliquer par des différences interspécifiques dans le comportement locomoteur et la charge sur les pieds.

[Traduit par la revue]

Introduction

Ungulates living in alpine habitats confront unusual challenges in the terrain they traverse and the weather they encounter. Mountain goats and bighorn sheep evolved to avoid predation by fleeing to precipitous terrain (Geist 1971; Schaller 1977). Level ground is scarce on the high-elevation landscapes inhabited by these animals. Moreover, at these elevations, snow can fall in substantial amounts during most of the year. Steep terrain and snow accumulation magnify the energy costs of travel (Parker et al. 1984; Fancy and White 1987). These costs, in turn, affect habitat choices of animals (Reichman and Atkinson 1981) and influence the energy surpluses they need for reproduction (Hudson and White 1985;

Fancy and White 1987). Thus, energy costs of locomotion on steep and snowy terrain emerge as potentially important controls on the distribution and abundance of mountain goats and bighorn sheep.

Although allometric relationships allow energy costs of locomotion for quadrupeds to be predicted solely on the basis of body size (Taylor et al. 1982), these relationships were developed for animals exercising on the level or on moderate inclines. Variation in environmental conditions and morphological differences among species may cause actual expenditures to diverge substantially from predicted ones (Fancy and White 1987). Because seasonal migrations by mountain goats are relatively brief, we expect selective pressure for efficiency in horizontal locomotion to be relaxed relative to species that annually migrate over long distances.

Here we examine the influence of conditions typically encountered in alpine environments on the energy costs of travel by bighorn sheep and mountain goats. We compare their efficiency of locomotion with previously reported values for

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mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and caribou (*Rangifer tarandus*).

Methods

We measured oxygen consumption ($\dot{V}O_2$) of three mountain goats (aged 5–22 months, weighing 12.4–50.8 kg) and five bighorn sheep (aged 6–23 months, weighing 22.0–68.9 kg) in response to different exercise regimes. These regimes included locomotion on a treadmill, on level and steep ground, and in snow of varying depths. Experimental animals were bottle raised. We used operant conditioning to train them to wear a harness and respiratory mask and to perform according to experimental protocols.

Oxygen consumption during horizontal locomotion was measured indoors on a treadmill and outdoors in snow and on asphalt and gravel roads. Oxygen consumption during vertical locomotion was measured outdoors on a 3.4° road and on a 21.5° stone and earthen dam. Conditions during measurement, including ambient temperature and altitude, varied among trials (Table 1). To avoid the confounding effects of temperature on $\dot{V}O_2$, measurements were not made if animals panted before exercising. Altitudes at work sites ranged from 1500 to 3233 m. Changes in altitude of this magnitude exert inconsequential effects on $\dot{V}O_2$ for standing and moderate exercise (reviewed by Consolazio et al. 1966 and di Prampero 1986).

We measured $\dot{V}O_2$ for locomotion on level and steep ground and in snow (these trials are hereafter referred to collectively as outdoor trials), using tight-fitting respiratory face masks and meteorological balloons (Kaysam Corporation, Patterson, NJ). Masks were made from variously sized plastic Erlenmeyer flasks chosen to match the circumference of each animal's muzzle. Each flask's base and neck were cut off, the flask was heated and compressed into an oval shape to better fit the animal's face, and the small end was covered with hard plastic. The conical shape reduced the dead-air space around the nares. To prevent air leakage, we lined the opening of the mask with foam rubber and a latex sleeve. We applied a water-insoluble gel to the sleeve opening each time the mask was used. Two V-valves (Warren E. Collins, Braintree, MA) were mounted on the side of the mask. Each valve was mounted with the diaphragm close (usually <5 cm) to the animal's nostrils to reduce dead-air space and allow free movement of the diaphragm under subfreezing conditions. One end of the valve tube was removed and the valve was cemented to the mask wall. The efficacy of the mask's seal was evaluated by measuring the oxygen concentration of the air around the base of the mask, using a vacuum pump to draw a continuous sample of air.

We measured volume and oxygen content of expired air collected in balloons with a wet-test gas meter (GCA Precision Scientific, Fisher Scientific) and paramagnetic oxygen analyzer (Beckman Instruments, Inc., Irvine, CA). Oxygen determinations were made on dried air (Drierite, Fisher Scientific, Pittsburgh, PA), and volume was corrected for standard temperature and pressure, dry. Expired air volume was corrected to inspired volume with an assumed respiratory quotient (RQ) of 0.82. We calibrated the oxygen analyzer with outdoor air and a reference gas mixture several times each day.

We measured $\dot{V}O_2$ during treadmill trials by means of loose-fitting masks and an open-circuit system. Initially, $\dot{V}O_2$ was determined by conventional methods. We calibrated the oxygen analyzer (Applied Technical Products, Denver, CO) with known gases and measured mass air flow through the animal's mask (Ventilation Measurement Module, Alpha Technologies Inc., Laguna Hills, CA). The air entering the oxygen analyzer was dried. An assumed RQ of 0.82 was used to correct expired air volume to inspired volume. To ensure that flow rates through the masks were adequate to recover all of the expired air, ventilation was first measured at each treadmill speed with the tight-fitting masks described above. These ventilation rates determined the minimum flow rates to be used with the open-circuit system. We further tested the adequacy of flow rates by increasing flow and examining rates of $\dot{V}O_2$. These procedures were later modified following Fedak et al. (1981). The air entering the analyzer was dried and CO_2 was removed (Ascarite, Fisher Scientific). A low-volume

TABLE 1. Conditions during measurements of O_2 consumption by exercising mountain goats and bighorn sheep

	Speed, km/h	Temperature, °C	Duration, s	Altitude, m
Horizontal				
Road	1.1–16.3	–10 to 18	15–180	1500–3248
Treadmill	1.7, 5.0, 8.4	11 to 24	180	1500
Slope				
4.0°	4.7–6.0	–3 to –6	30–400	3300
21.5°	2.5–5.8	–5 to 20	25–87	1500
Snow	1.1–9.0	–10 to –6	24–132	1500–3248

flowmeter (Gilmont, Cole-Parmer Instrument Company, Chicago, IL), previously calibrated with a Brooks Volumeter, was used to measure nitrogen flow into the respiratory masks. We used eq. 11c of Fedak et al. (1981) to calculate $\dot{V}O_2$.

Like Cohen et al. (1978) and Parker et al. (1984), we found that a 1-min pretrial allowed exercise effort and respiratory gas characteristics to reach equilibrium. Thus, expiratory gas collection was initiated after 1 min of exercise for outdoor trials and after 2 min for treadmill trials. The extra pretrial time in treadmill trials was needed to allow the treadmill to reach the desired travel speed.

We observed animals lying and standing to assess the energy costs of maintaining posture. We eliminated any observations that included activity above the standing or lying state (moving the head, pawing the ground, etc.).

To assess costs of travel on level surfaces we regressed $\dot{V}O_2$ on travel speed for each animal and used the slope of the regression to estimate the net cost of locomotion. We pooled data from measurements from outdoor and treadmill trials. Differences between slopes of regressions for outdoor and treadmill measurements were small and usually nonsignificant. Regressions calculated in this way do not represent steady-state respiratory conditions (Taylor et al. 1982) or moderate-effort conditions (Fancy and White 1987). We justify pooling these data, however, because this provides a more adequate sample size and enhances consistency with outdoor measurements made in snow and on slopes (e.g., high levels of $\dot{V}O_2$, timing and duration of measurements).

Estimating the net energy cost of uphill locomotion (E_{up}) proved problematic. The classical approach of Taylor et al. (1972) calculates E_{up} as

$$[1] E_{up} = \frac{(S_{up} - S_{level}) \cdot 20.19}{\sin \Theta}$$

where E_{up} (J/(kg · m)) is the energy cost of raising 1 kg of body weight one vertical metre, S_{up} is the net cost (mL O_2 /(g · km)) of walking uphill (slope of regression measured $\dot{V}O_2$ and travel speed (km/h)), S_{level} is the net cost of horizontal locomotion (mL O_2 /(g · km)), 20.19 is the energy equivalent of oxygen (J/mL O_2) at the assumed RQ of 0.82, and $\sin \Theta$ is the fraction of a metre climbed per metre traveled. However, regressions of $\dot{V}O_2$ on travel speed were exceedingly difficult to develop for the 21° slope because the range of observed speeds was limited by the animal's reluctance to travel rapidly on steep inclines. Intercepts of some regressions were substantially negative. Consequently, we do not have faith in the inferences offered by these equations. Alternatively, we used speed-specific estimates of $\dot{V}O_2$ (the quotient of (mL O_2 /(g · h)) divided by travel speed (km/h)) instead of slopes of regressions to estimate S_{up} in the above equation. Using this approach, we obtained a value for each trial and averaged values across trials for each animal. The problem with this alternative is that speed-specific travel costs decrease with increasing speed (Taylor et al. 1970). Although this problem is mitigated by the narrow range of speeds achievable on steep slopes, we urge caution in applying our values to speeds that depart from those we observed. The efficiency of the work of walking

uphill was calculated by dividing 9.79 (joules potential energy in a 1-kg object raised 1 m) by E_{up} .

Speed-specific energy expenditure for walking downhill, E_{down} , was calculated as

$$[2] E_{down} = \frac{(C_{level} - C_{down}) \cdot 20.19}{\sin \Theta}$$

where E_{down} (J/(kg · m)) is the energy recovered upon lowering 1 kg of body weight 1 m, C_{level} is the speed-specific cost (mL O₂/(kg · m)) of locomotion on level ground, defined as VO_2 at a specific speed divided by that speed, C_{down} is the speed-specific cost (mL O₂/(kg · m)) of locomotion down a slope, defined as VO_2 at a specific speed divided by that speed, and $\sin \Theta$ is the fraction of a metre descended per metre traveled. The efficiency of the recovery of potential energy while descending was calculated by dividing E_{down} by 9.79 (Fancy and White 1987).

We assumed in calculating E_{up} and E_{down} that animals could be viewed as moving along the hypotenuse of a right-angled triangle. Thus, for eq. 1 and 2, we used $\sin 21.5$ (0.37) in the denominator rather than percent slope (0.39, i.e., $\tan 21.5$).

VO_2 for locomotion in snow was determined by leading animals wearing respiration equipment through flat, undisturbed snow. Our protocol for leading animals followed Parker et al. (1984). Procedures for morphological measurements of animals (brisket height and foot area) also followed Parker et al. (1984). We measured snow density by weighing samples collected in a thin-walled, 6 cm diameter plastic cylinder of known volume thrust into the snow to the level of animal penetration. Animal penetration was measured with a metre stick inserted into the sample track. Interspecific comparisons of VO_2 were based on observations in uncrusted snow.

We assumed that the relationship between travel speed and VO_2 was linear for all treadmill and outdoor trials on hard surfaces. This assumption is supported by the findings of others (Taylor et al. 1982; Parker et al. 1984; Fancy and White 1987), as well as by our own observations.

Snow density was confounded with sinking depth. (Deep snow tended to be less dense than shallow snow.) Nonlinear least-squares approximations of the multivariate model of Parker et al. (1984, Fig. 7) to our data on snow depth and density failed to converge over a broad range of initial conditions, using two different curve-fitting algorithms. Alternatively, we used analysis of covariance, with density as a concomitant observation for sinking depth, to adjust animal responses to the same average snow density (0.19 g/cm³ for mountain goats, 0.17 g/cm³ for bighorn sheep) over all sinking depths. We report values for energy expenditure adjusted and unadjusted by the covariate. We used the algorithm of false position (Ralston and Jennrich 1978) to fit models to nonlinear data. The standard error of the estimate for an additional measurement of the independent variable (X , at the mean X) of regressions was calculated with eq. 33 of Zar (1973). We used one at a time confidence intervals to examine interspecific differences in coefficients of linear and nonlinear models.

Results

Incremental cost of standing

Increments in VO_2 for standing over lying ranged from 23 to 29% for sheep and goats. These values resemble those observed for many other ungulates (Fancy and White 1987, Table 1) but exceed those previously observed for bighorn sheep (18%, Chappel and Hudson 1979). Because animals were relaxed and had been inactive before and during measurements, we are confident that these increments reflect differences in posture uninfluenced by activity.

Movements such as lifting the legs or moving the head substantially increased VO_2 . For example, consecutive VO_2 measurements of one bighorn sheep changed from 0.745 mL O₂/(g · h) when it stood and frequently moved its head and

legs, to 0.532 when it stood with less frequent movement, to 0.284 when it lay down and rested its head on the ground. In this series of activities, standing with minor activity required 86% more energy than relaxed and motionless recumbency. These observations emphasize the fundamental importance of standardizing observations of the lying and standing state when measuring incremental costs.

Locomotion on hard surfaces

We found highly significant ($P < 0.001$) linear relationships between VO_2 (mL O₂/(g · h)) and speed (km/h) for each subject moving horizontally (Table 2). Net costs of locomotion (slopes of regressions) (mL O₂/(g · km)) ranged from 0.24 to 0.28 and varied little between sheep and goats of similar body weights. Our findings resembled net costs for horizontal locomotion reported for domestic sheep, white-tailed deer, and elk calves (reviewed by Fancy and White 1985, Table 3) but were about 25% higher than the interspecific average predicted for *Artiodactyla* (Taylor et al. 1982) and almost 300% higher than values observed for migratory ungulates (reviewed by Fancy and White 1985, Table 3).

On average, the slopes of regressions based on pooled data from treadmill and ground measurements were about 7% steeper than slopes calculated from steady-state measurements on the treadmill, 0.26 vs. 0.24 mL O₂/(g · km). This discrepancy probably resulted from the softer outdoor surfaces (White and Yousef 1977), experimental difficulties at higher travel speeds (Fancy and White 1987), and differences in VO_2 measurement systems or protocol. Speed-specific energy costs of lifting 1 kg through one vertical metre (E_{up}) on the 3.4° slope were 18.67 J/(kg · m) for sheep T1 and 14.42 J/(kg · m) for goat N1 (Table 3). These costs are well within the range (2.02–27.03) reported for other species on inclines lower than about 6° (Cohen et al. 1978; Fancy and White 1987). On the 21.5° slope, energy costs of lifting 1 kg through one vertical metre (E_{up}) averaged 38.2 (±3.7) J/(kg · m) for sheep and 37.07 (±0.69) J/(kg · m) for goats (Table 3). Our observations of the efficiency of uphill locomotion costs for sheep and goats (23–29%) are in the lower range of values seen for most large quadrupeds (23–81%; reviewed by Cohen et al. 1978).

Speed-specific costs of walking down a 21.5° slope were extremely variable (Table 4). Four of six animals expended more energy walking downhill than on the level. Downhill oxygen cost per unit of distance walked averaged 1.08 times greater than horizontal cost for these four subjects. The two subjects that recovered energy walking downslope did so with efficiencies (21 and 28%) that were substantially lower than the range reported (54–72%) for similar sized (ca. 49 kg) elk on moderate inclines (4.2–14.3°) (Cohen et al. 1978; Parker et al. 1984). Numerous studies report that efficiency decreases as the incline increases (reviewed by Parker et al. 1984). The only other test of steep downslope locomotion was made with humans. As with our findings, humans began to expend more energy walking downhill than moving horizontally when inclines exceeded 18° (Taylor et al. 1972). Humans expended 1.5 times more energy moving down a 40% slope than they did moving on a horizontal surface (Margaria 1976, p. 71).

Locomotion in snow

Contrary to the observations of others (Mattfeld 1974; Parker et al. 1984; Fancy and White 1987), we found that the relative increase in the net cost of locomotion (RINCL) in snow failed to increase continuously and exponentially as sinking depth increased (Fig. 1). Instead, the relative increase in

TABLE 2. Linear regressions ($Y = a + bX$) relating VO_2 (Y , mL O_2 /(g · h)) by bighorn sheep and mountain goats to travel speed (X , km/h) for a horizontal hard surface

	Weight ($\bar{x} \pm SD$), kg	Speed, km/h	Regression coefficient		n	r^2	P	SE_{est}
			a	b				
Sheep								
T1	29.4±3.2	3.3–10.9	0.37	0.25	5	99	0.001	0.08
R1	39.2±2.2	1.7–14.1	0.31	0.24	22	89	0.001	0.25
C1	40.6±1.1	1.7–16.3	0.42	0.25	20	92	0.001	0.29
A2	67.3±1.6	1.7–14.8	0.13	0.24	27	83	0.001	0.38
Goats								
S1	15.3±1.7	1.7–8.4	0.58	0.28	26	90	0.001	0.23
NB1	25.2±1.7	1.7–11.2	0.50	0.26	11	88	0.001	0.30
B1	32.2±3.8	1.7–15.2	0.57	0.24	30	90	0.001	0.30
N2	45.3±3.3	1.7–14.8	0.26	0.26	23	95	0.001	0.22

NOTE: Letters identify individual animals; 1 denotes a lamb or kid, 2 denotes a yearling; a , estimated VO_2 while standing (mL O_2 /(g · h)); b , net cost of locomotion (mL O_2 /(g · km)); SE_{est} , is the standard error for the estimate of a new observation at the mean travel speed.

TABLE 3. Energy expenditures by bighorn sheep and mountain goats traveling uphill

	Angle, deg.	Mass, kg	Speed, ($\bar{x} \pm SD$), km/h	n	Vertical cost		Efficiency	
					mL O_2 /(g · km)	Multiple of level cost	E_{up}^a , J/(kg · m)	%
Sheep								
T1	3.5	27.0	5.4±0.3	11	0.37	1.16	18.67	52.4
T1	21.5	31.4	3.1±0.5	6	1.02	2.76	35.47	27.6
M1	21.5	39.0	2.7±0.0	1	1.05	2.76	36.56	26.8
C1	21.5	40.6	3.6±0.4	3	0.98	2.65	33.29	29.4
R1	21.5	40.9	3.6±0.0	2	1.05	3.18	39.29	24.9
A1	21.5	49.5	3.2±0.4	3	1.15	3.19	43.11	22.7
A2	21.5	68.6	3.1±0.8	2	1.04	3.71	41.47	23.6
Mean ^a					1.05		38.20	25.8
SE					0.06		3.75	2.5
Goats								
N1	3.4	23.7	5.2±0.4	9	0.40	1.12	14.42	67.9
S1	21.5	16.1	3.6±0.0	1	1.13	2.57	37.65	26.0
N1	21.5	29.5	3.5±0.0	1	1.06	2.65	36.02	27.2
B1	21.5	35.7	3.8±0.3	5	1.10	2.82	38.74	25.3
N2	21.5	42.0	3.3±0.2	3	1.00	2.94	35.88	27.3
Mean ^a					1.07		37.07	26.4
SE					0.03		0.69	0.5

NOTE: Letters identify individual animals; 1 denotes a lamb or kid, 2 denotes a yearling.

^aAverage of values for 21.5° slope.

locomotory costs reached an asymptote when sinking depth exceeded roughly 1.2–2 times the animal's brisket height.

The effect of sinking depth on RINCL depended on snow density (Fig. 1), but was substantially greater for mountain goats than for bighorn sheep. We could detect no difference in asymptotic maximum values (adjusted for snow density) for RINCL between species (95% confidence interval (CI) = 437–479% for bighorn sheep, 412–529% for mountain goats). The rate of approach to the asymptote, however, was more rapid in bighorn sheep (95% CI = 0.04–0.06%/cm) than in mountain goats (95% CI = 0.02–0.03%/cm). As a result of this difference in rates, values for RINCL in bighorn sheep were less than those for mountain goats when sinking depths were less than 78% of the brisket height, but exceeded them when the snow was deeper.

Morphological characteristics also influenced the efficiency

of travel in snow. Efficiency of travel in snow is influenced by the brisket height and foot loading. Brisket heights of bighorn sheep exceeded those of mountain goats (Fig. 2) and thereby offered an anatomical advantage for travel when snow depths encountered by the two species were equal. However, the advantage conveyed to bighorn sheep by their higher brisket height was somewhat offset by a disadvantage in foot loading (Fig. 3). This disadvantage resulted because foot area of bighorn sheep tended to be less than that for mountain goats of similar weight (Fig. 4). As a result of the trade-offs between brisket height and foot loading, RINCL as a function of absolute sinking depth was similar for the two species (Fig. 4).

Discussion

Bighorn sheep and mountain goats traveled in snow effi-

TABLE 4. Energy expenditures by bighorn sheep and mountain goats walking down a 21.5° incline

	Mass, kg	Speed ($\bar{x} \pm \text{SD}$), km/h	n	Vertical cost		Efficiency	
				mL O ₂ /(kg · m)	Multiple of level cost	E_{down}^a J/(kg · m)	%
Sheep							
T1	35.2	5.0 ± 1.1	2	0.27	0.84	2.73	28
R1	40.9	4.2 ± 0.2	2	0.33	1.05	-0.82	-8
C1	42.4	3.6 ± 0.0	1	0.42	1.14	-2.73	-28
A2	68.6	4.5 ± 0.3	2	0.29	1.07	-1.09	-11
Goats							
B1	35.8	4.6 ± 0.7	2	0.39	1.08	-1.53	-16
N2	42.0	3.5 ± 0.8	2	0.30	0.89	2.07	21

NOTE: Letters identify individual animals; 1 denotes a kid or lamb, 2 denotes a yearling. Vertical costs are calculated as V_{O_2} at a given speed (mL O₂/(g · h)) divided by that speed (km/h); the multiple of level cost is computed with horizontal costs derived from each subject's regression estimate at the speed of interest.

^aA negative value indicates that downhill cost exceeded horizontal cost.

ently, but showed no apparent adaptation for travel on steep terrain. Findings on the effect of angle of ascent on the efficiency of locomotion are equivocal. Others have concluded that angle has no effect on efficiency (Robbins 1983, p. 116; Fancy and White 1987), that angle and efficiency are negatively correlated (Parker et al. 1984), and that extreme variation among studies precludes formation of generalizations about efficiency of locomotion on slopes (Cohen et al. 1978). Our observations suggest that efficiency decreases (E_{up} increases) with increasing angle of ascent. Efficiencies of locomotion for sheep and goats on the 21.5° incline, which is the steepest slope tested for quadrupeds, were generally lower than any documented for animals >1 kg traveling on more moderate inclines (reviewed by Cohen et al. 1978; Fancy and White 1985). Speed-specific oxygen consumption per unit of distance traveled up the 39% slope averaged about 2.8 times greater than costs for walking horizontally at the same speed for bighorn sheep and mountain goats. Although these increases are large, they are substantially less than the 7.6-fold increment shown by humans walking up a 40% slope (Margaria 1976, p. 71).

Increments between vertical and horizontal costs were greater for heavier animals than for lighter animals. As noted by Taylor et al. (1972), this results from the fact that smaller animals have relatively higher weight-specific costs of horizontal locomotion, whereas vertical costs remain largely uninfluenced by body size.

Animals inhabiting alpine terrain could expend inordinate energy for locomotion relative to animals that travel on level landscapes if they traversed similar distances on those different surfaces. However, even though travel on steep terrain is costly per unit distance, animals can save energy in their daily movements by choosing steeper ascents, thereby reducing the amount of time and distance they travel. The cost of moving up steep inclines can be less than the cost of traveling farther on a shallower incline (Reichman and Atkinson 1981). For example, comparing 21.5 and 3.4° inclines and considering the speeds typically traveled by our animals (about 3.3 km/h for the 21.5° incline and 5.3 km/h for the 3.4° incline), sheep or goats choosing to walk up the shallower slope would travel 525% farther to attain the same elevation, and would expend about 131% more energy (2.2–5.0 J/kg for sheep T1 and 2.3–5.4 J/kg for goat N1). However, if the efficiency of travel on inclines decreases as the slope increases, there will

be an optimum angle of ascent that will yield the lowest cost for travel between two points, an optimum that compromises distance traveled against the inefficiency of an exceedingly steep angle of travel.

Our observations of an asymptote in the relationship between energy expenditure and relative sinking depth contrasts with the exponential increase observed by others. Previous workers limited their observations to sinking depths shallower than those we observed. This is probably realistic for cervids who routinely avoid deep snow by migrating (e.g., Sweeney and Sweeney 1984) or by concentrating in "yards" (Mattfeld 1974). However, it is not uncommon for alpine ungulates to confront snow depths that are substantially deeper than their brisket heights, particularly after storms and before winds have cleared exposed ridge tops.

Rigorous comparison of our findings on the effects of snow with those seen for other ungulates is made difficult by differences in the models used to fit the data. Despite this problem, we can surmise qualitatively that the increase in RINCL as a function of sinking depth in bighorn sheep resembled relationships for cervids, but that the functional form of RINCL in mountain goats departed substantially from cervid curves (Fig. 5). We explain this departure on the basis of locomotory behavior. The rapid acceleration in RINCL when sinking depth exceeds the height of the carpus has been attributed to restriction of leg movement and increased drag (Fancy and White 1987). However, at depths between the heights of the carpus and the brisket, we observed that bighorn sheep tended to change from a walking gait to "bounding" through the snow, a shift that has also been seen in cervids (Mattfeld 1974, p. 149; Parker et al. 1984). Unlike other ungulates, mountain goats continued to walk, regardless of snow depth. Even when sinking depth exceeded their brisket height they "plowed" through the snow, whereas bighorn sheep leapt through it. This difference in behavior can explain the relative efficiency of mountain goats traveling in deep snow (Fig. 5), as well as their sensitivity to the effects of snow density (Fig. 1). Bounding is energetically costly (Mattfeld 1974, p. 149; Parker et al. 1984) because it requires vertical as well as horizontal movement. However, the bounding animal avoids contact with the snow, unlike the animal plowing through it, and consequently is less sensitive to changes in snow density. We emphasize, however, that although this behavior allowed mountain goats to travel more efficiently than bighorn sheep at the same rela-

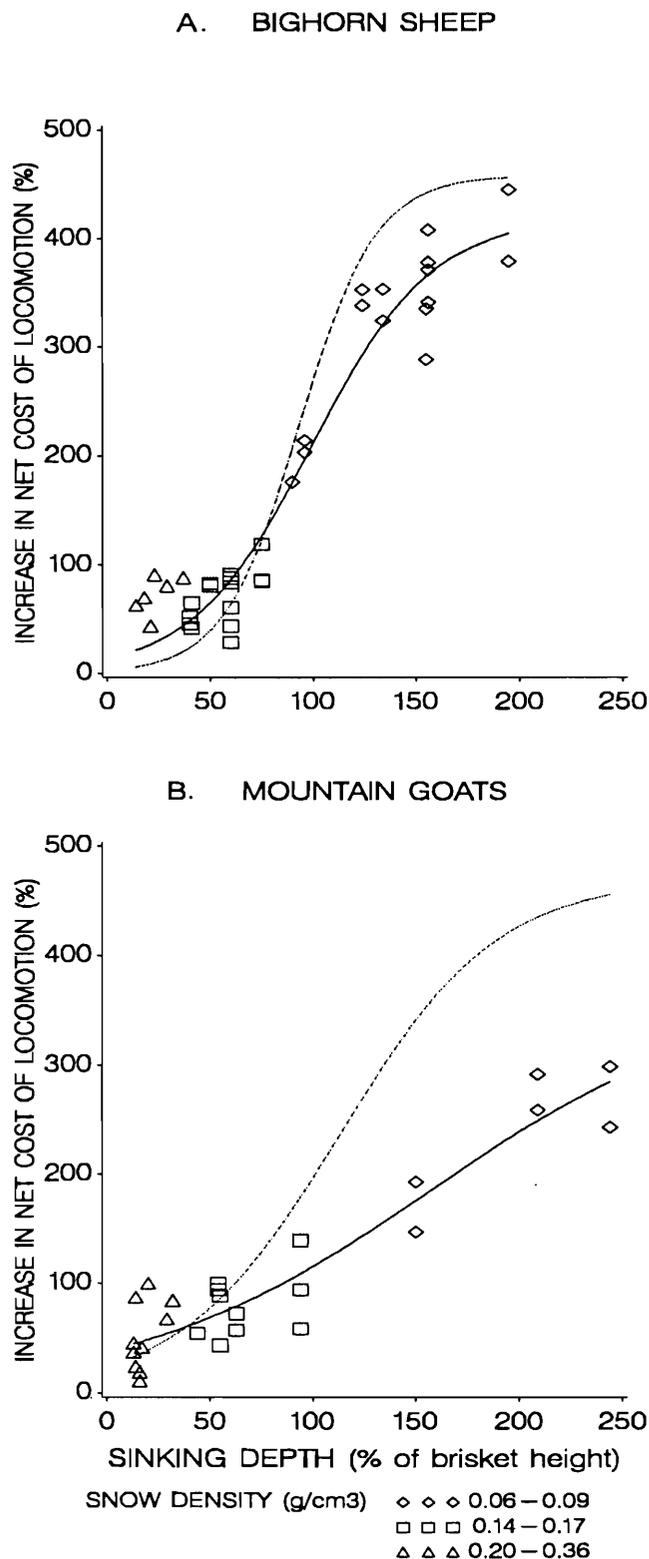


FIG. 1. The relative increase in the net cost of locomotion as a function of relative sinking depth for alpine ungulates in uncrusted snow of different densities. (A) Solid line shows the fit to observed data for bighorn sheep ($y = 421/(1.0 + 29.7 \cdot e^{(-0.034 \cdot x)})$, $SE_{est} = 35.6$). Broken line shows the fit for data adjusted by covariance to the average snow density of 0.17 g/cm³ ($y = 458/(1.0 + 156 \cdot e^{(-0.054 \cdot x)})$, $r^2 = 0.99$, $SE_{est} = 22.4$). (B) Solid line shows the fit to observed data for mountain goats ($y = 374/(1.0 + 8.88 \cdot e^{(-0.013 \cdot x)})$, $r^2 = 0.96$, $SE_{est} = 29.9$). Broken line shows the fit to data adjusted by covariance to the average snow density of 0.019 g/cm³ ($y = 471/(1.0 + 18.7 \cdot e^{(-0.026 \cdot x)})$, $r^2 = 0.98$, $SE_{est} = 10.9$).

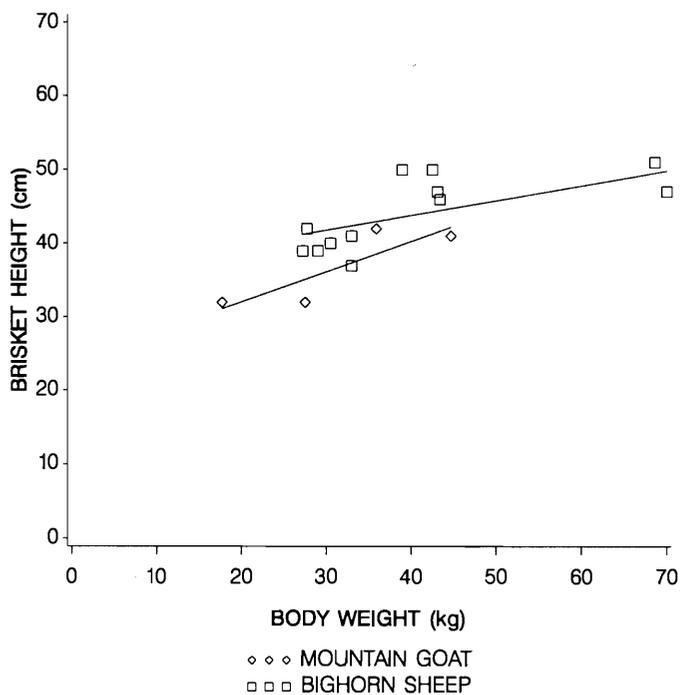


FIG. 2. Brisket height in mountain goats and bighorn sheep relative to body weight. The equation for bighorn sheep is $y = 35.7 + 0.20x$ ($r^2 = 0.56$, $SE_{est} = 2.14$); the equation for mountain goats is $y = 23.9 + 0.41x$ ($r^2 = 0.74$, $SE_{est} = 2.05$).

tive sinking depth (Fig. 1), absolute efficiencies were not different (Fig. 4).

The most striking feature of the energetics of travel in mountain goats and mountain sheep was their inefficiency compared with other ungulates. The energy costs of locomotion by mountain goats and bighorn sheep exceeded values for the Artiodactyla in general (Taylor et al. 1982), and specifically exceeded values observed in migratory ungulates by a factor of 3 (Fancy and White 1987). Extensive travel selects for efficiency in locomotion (Fancy and White 1987); however, although mountain goats and bighorn sheep may migrate seasonally, these movements are relatively short. Legs (measured at brisket height, Fig. 2) of mountain goats and bighorn sheep were shorter relative to body mass than those of cervids (Parker et al. 1984; Fig. 3; Fancy and White 1987, Fig. 4). Moreover, the leg bones of alpine ungulates are thicker relative to their length than the leg bones of caribou (McMahon 1973). These morphological differences offer an explanation for the relative inefficiency of travel of alpine ungulates; long legs convey advantages for steady locomotion by allowing elastic storage of energy (Alexander 1979). Thin limbs enhance this advantage by reducing weight.

Locomotion in mammals has evolved in response to two selective pressures, the need to travel and the need to escape. Animals that avoid being eaten by fleeing to proximal cover must be able to increase their velocity rapidly, even if this ability detracts from their efficiency of travel. Bighorn sheep and mountain goats escape from predators by rapid flight to inaccessible terrain. Their flight frequently requires jumping up and down steep inclines, which places much greater stress on limbs than horizontal movement (Alexander 1974; Alexander et al. 1979). Long legs offer no mechanical advantage for rapid acceleration and jumping (Alexander 1979). However, short thick leg bones are less likely to bend and break on

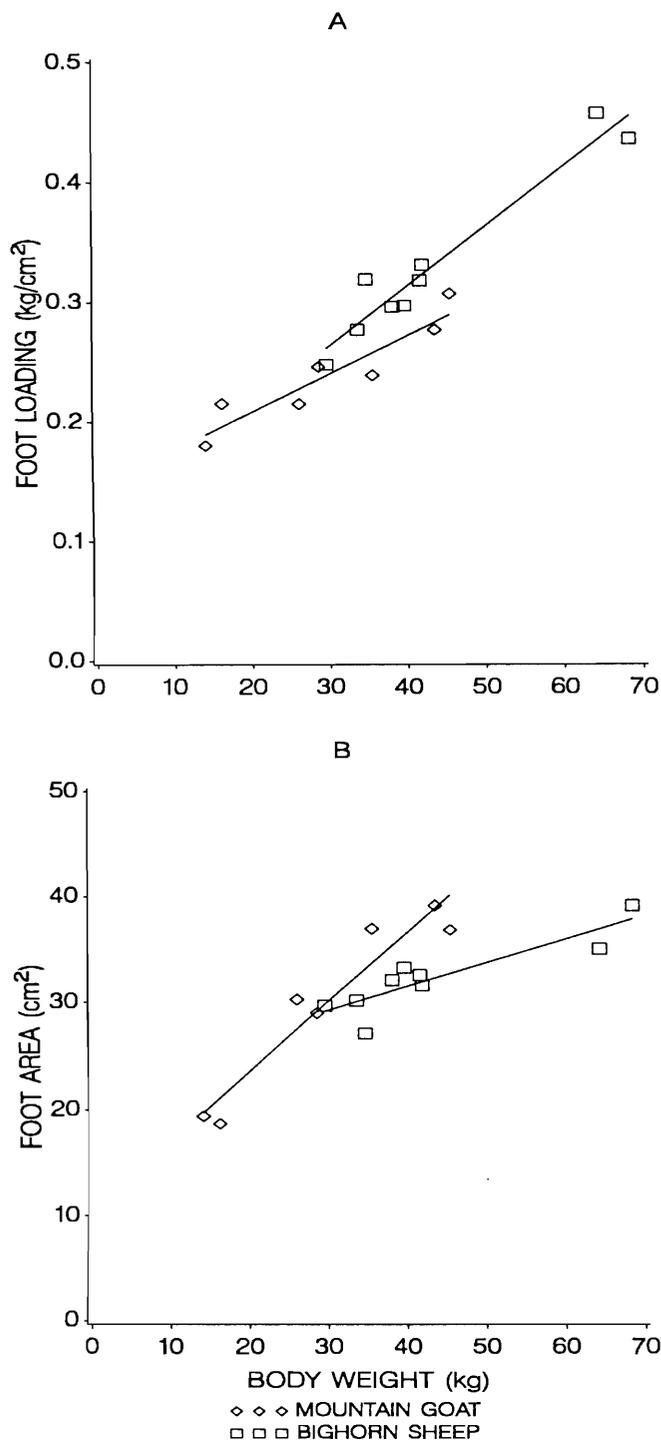


FIG. 3. (A) Foot loading in mountain goats and bighorn sheep relative to body weight. The equation for bighorn sheep is $y = 0.11 + 0.005x$ ($r^2 = 0.87$, $SE_{est} = 0.15$); the equation for mountain goats is $y = 0.14 + 0.003x$ ($r^2 = 0.93$, $SE_{est} = 0.15$). (B) Foot area in mountain goats and bighorn sheep relative to body weight. The equation for bighorn sheep is $y = 10.6 + 0.65x$ ($r^2 = 0.78$, $SE_{est} = 1.53$); the equation for mountain goats is $y = 10.6 + 0.65x$ ($r^2 = 0.91$, $SE_{est} = 1.92$).

impact than long thin ones (Currey 1967). Thus, we suggest that the relative inefficiency of travel in alpine ungulates represents an evolutionary compromise between the need to travel and the need to escape to precipitous terrain.

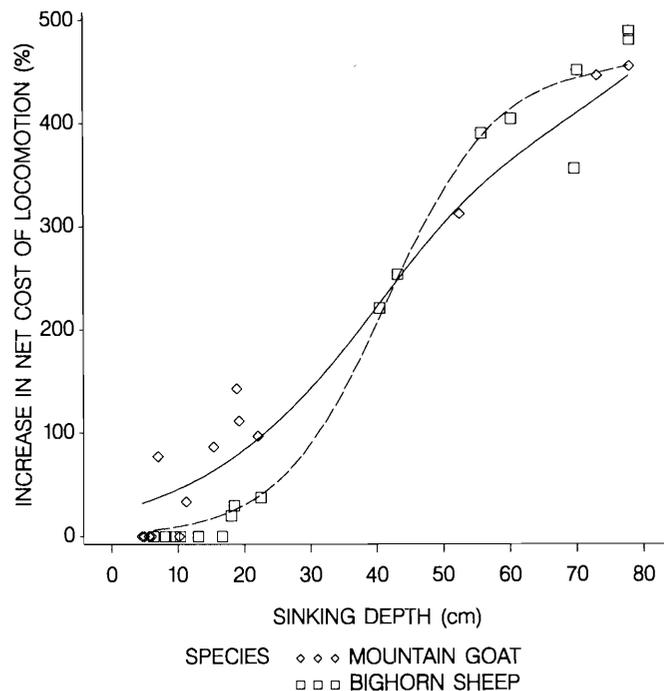


FIG. 4. The relative increase in the net cost of locomotion for bighorn sheep (broken line, $y = 458 / (1.0 + 156 \cdot e^{0.12 \cdot x})$, $r^2 = 0.99$, $SE_{est} = 22.4$) and mountain goats (solid line, $y = 471 / (1.0 + 18.7 \cdot e^{-0.073 \cdot x})$, $r^2 = 0.89$, $SE_{est} = 34.6$) as a function of absolute sinking depth. Curves are adjusted to average snow densities of 0.17 g/cm^3 for bighorn sheep and 0.19 g/cm^3 for mountain goats.

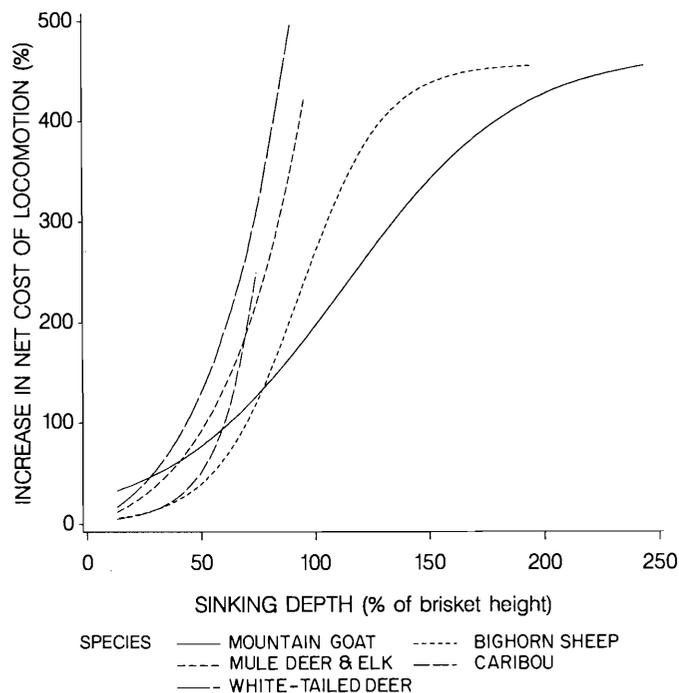


FIG. 5. The relative increase in the net cost of locomotion for North American ungulates as a function of relative sinking depth. Curves for bighorn sheep and mountain goats are adjusted to average snow densities of 0.17 g/cm^3 for bighorn sheep and 0.19 g/cm^3 for mountain goats. Snow densities during measurements of other ungulates were 0.20 g/cm^3 for mule deer and elk (Parker et al. 1984) and $0.14\text{--}0.20 \text{ g/cm}^3$ for caribou (Fancy and White 1987). Snow density for white-tailed deer was unknown (Mattfeld 1974).

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