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ENERGY EXPENDITURES FOR LOCOMOTION BY MULE DEER AND ELK

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Abstract: Energy expenditures for several activities were measured using indirect calorimetry with five mule deer (*Odocoileus hemionus*) and eight elk (*Cervus elaphus nelsoni*). The average energetic increment of standing over lying was 25%. Net energy costs (kcal/kg/km) of horizontal locomotion without snow decreased as a function of increasing body weight. The average cost per kilogram for each vertical meter climbed on a 14.3° incline was 5.9 kcal. Efficiency of upslope locomotion averaged 40–45% for the two species; downslope efficiency decreased with increasing body size. Energy expenditures for locomotion in snow increased curvilinearly as a function of snow depth and density. To further understand the energetics of locomotion in snow, foot loading and leg length were measured. Management implications, based on the costs of locomotion for mule deer and elk when disturbed by winter recreationists and when traversing the slash deposition of logging operations, are discussed.

The adaptability of an animal to its environment is subject to the energetic constraints that direct its activity patterns and foraging strategies. While energy may not be a limiting factor during all seasons, it is of particular importance in the winter survival of many free-ranging ungulates. Extensive mortality is often indicative of the interplay between increased energy expenditures and decreased forage quality and availability.

In recent years, there has been a proliferation of bioenergetic studies examining the energy costs of locomotion for a variety of mammals (Taylor et al. 1970, 1972; Schmidt-Nielsen 1972; Fedak et al. 1974; Wunder 1975; Chassin et al. 1976; Taylor 1977; Cohen et al. 1978). Since most bioenergetic studies have been conducted on domestic animals or in the laboratory, there exists a need for investigations of wild ungulates in their natural surroundings. Knowledge of energy expenditures for locomotion will further our comprehension of the constraints within which animals use their environment. Captive mule deer and elk are particularly suitable for such investigations since they are easily trained for respiratory gas collections.

Specific objectives of this study were: (1) determine the energetic costs of lying, standing, and horizontal and vertical locomotion for captive mule deer and elk using indirect calorimetry; quantify the net energy cost (kcal/kg/km) of locomotion; evaluate these expenditures in terms of efficiency (mechanical work done relative to energy expended); (2) analyze the effects of snow depth and density on energy expenditure; evaluate differences in the cost of locomotion in snow relative to foot area, body weight, brisket height, and velocity of travel; and (3) provide estimates of energy expenditures by wild ungulates upon which management of deer and elk in deep snowfall regions and logged forests can be based.

lowstone Natl. Park and the U.S. For. Serv. Range and Wildl. Habitat Lab. in La Grande, Oreg. Mule deer fawns were supplied by Wash., Idaho, Oreg., Colo., and Wyo. wildlife agencies. We are grateful to L. D. Bryant, D. A. Leckenby, M. M. Meagher, R. A. Parker, D. W. Spirtes, and J. W. Thomas for support and services. The technical assistance of L. L. Boyd, D. T. Cancellare, J. A. Gaulke, S. J. Hartwick, J. L. Hill, D. A. Julian, A. R. Pfister, and M. A. Reisenauer in the care and handling of experimental animals and the construction of specialized equipment is appreciated.

METHODS

Mule deer fawns and elk calves were bottle-raised singly in small, protected pens. Growth rates of these animals were comparable to those of maternally raised neonates (Robbins et al. 1981). After weaning at 3 months of age, all animals had ad libitum access to excellent quality, third-cutting alfalfa hay. The deer were also fed an additional grain supplement. Beginning at 2 weeks of age, animals were trained to tolerate lead ropes and practice face masks consisting of a small plastic cup attached to an elastic strap. Such practice masks were worn by the animals for 2–3 hours/day until habituation was sufficient and the animals were large enough to begin training with actual respiratory masks.

Respiratory masks were constructed from nalgene or aluminum beakers lined with foam rubber padding and either latex or neoprene sleeves to prevent air leakage. The size of the beaker ranged from 40 to 4,000 ml, depending on animal size. Valve systems, containing two, four, or six disc valves (W. E. Collins, Braintree, Mass.), were attached to the end of the face masks and selected relative to weight limitations and the animal's oxygen demand. Respired air was collected for a

timed interval by means of spiral plastic tubing in neoprene meteorological balloons (Kaysam Corp., Patterson, N.J.).

Air samples were evacuated from neoprene balloons using two pressure-vacuum pumps (Neptune Dyna-Pump) at a flow rate measured with two Gilmont flowmeters that had been previously calibrated by water displacement. Total gas volume was calculated from the known flow rate and the time necessary to empty the balloons. Oxygen content was determined with a Taylor Servomex analyzer, calibrated prior to each series of air samples with nitrogen (0% oxygen) and atmospheric air (20.93% oxygen). Calculations of energy expenditure were based on an RQ of 0.82 (Brody 1945), a caloric equivalent of 4.83 cal/ml O_2, and corrections for standard temperature and pressure (Consolazio et al. 1963). All metabolic measurements were made on fully fed animals.

To assess the energetic increment between standing and lying, animals were trained to rest quietly in both positions while wearing the appropriate respiratory equipment. All measurements on lying animals were taken within the animal's pen to ensure minimum distraction and disturbance. Values from standing animals were measured both within the pens and at the sites of all locomotion studies. Metabolic costs of standing and lying were compared for only those values obtained sequentially on the same day to minimize the effect of body weight and feed intake changes.

Training for locomotion measurements was similar to that described by Cohen et al. (1978) and Robbins et al. (1979). Calves and fawns were tethered behind or to the side of a truck with a neck collar and lead rope and trained to follow at a variety of velocities. Use of a truck provided some security to a hesitant animal and regulat-

ed its velocity of travel at a constant pace. The animals were habituated to this experimental protocol by bottle-feeding them from the tailgate of a moving vehicle. Subsequent training involved exercising them daily behind the truck at different speeds and distances until no stress or lack of cooperation was apparent. The training period differed among animals, but in general averaged 1 month for elk calves and at least 2 months for mule deer fawns. Training and experiments during the summer were confined to early morning hours to avoid high ambient temperatures and induced thermal stress. Data for horizontal locomotion were collected from five mule deer (14–67 kg) and eight elk (28–148 kg), all less than 18 months of age. Oxygen use was determined for an average of nine different velocities/animal of a given body weight.

During studies of vertical locomotion on a 14.3° slope, elk calves were exercised behind a truck as for horizontal locomotion. Mule deer fawns were trained to walk between three investigators at a constant, predetermined pace. Animals were exercised downhill, rested, and then exercised uphill (Cohen et al. 1978). Data for vertical locomotion were obtained from five mule deer fawns (14–24 kg) and five elk calves (28–145 kg). The animals became increasingly reluctant with age to run uphill. For each animal, energy expenditures were examined as a function of seven different velocities of travel.

Preliminary studies of mule deer fawns indicated that a 1-minute pretrial was adequate for the equilibration of exercise effort and respiratory gas characteristics. While this conforms with earlier methods using the same equipment on elk calves (Cohen et al. 1978), periodic collections following longer pretrials (1.5 and 2.0 min) were routinely made throughout the study to determine if a 1-minute pretrial re-

mained sufficient for larger animals and gait changes. Oxygen use values determined with longer pretrials did not differ from those made at 1 minute.

The energy cost of locomotion in snow was determined for five elk (76–149 kg) and four mule deer (34–63 kg), transported either to Yellowstone National Park or La Grande, Oregon. Each animal was trained to walk in deep snow between two investigators wearing snowshoes. A third person traveled behind the animal to ensure that it maintained a constant pace. All training and data collection occurred at ambient temperatures within the thermoneutral zones of calves and fawns (Gates and Hudson 1979). Animals were taken by trailer to relatively flat snowfields of uniform, noncrusted snowpack that were large enough that each animal could be exercised in undisturbed snow at four or five different velocities. Twenty-six different snow depths, measured to the nearest cm (13–62 cm), were used. Snow density was determined by pushing a thin-walled, 12-cm-diameter aluminum cylinder into the snowpack to a depth equal to the animal's sinking depth and weighing its contents.

Because the cost of locomotion in snow was expected to be a function of sinking depth (Mattfeld 1974), brisket height, carpus or front knee height, and tarsus or hock height were measured from ground surface (nearest cm) and correlated with body weight. Foot area was also determined by photographic projection. Defined as the area which faces downward in a normal stance (Telfer and Kelsall 1979), foot area included the bottom of the hoof and the phalanx up to and including the dewclaws. A wooden platform containing a glass window was constructed and placed over the opening to an underground cellar. Positioning the animal with one foot on the glass surface enabled

an investigator to photograph the bottom of the foot from beneath. All photographs were taken at a minimum of 1.5 m from the object to avoid the problems of parallax. When the images were projected to true size, based on a scaling marked on the glass window, the perimeter of the foot, excluding the area between the toes, was traced on paper and the image excised. The area of these paper replicates was then determined to the nearest 0.01 cm^2 using a Li-cor portable area meter (Lambda Instruments Corp., Lincoln, Nebr.).

RESULTS AND DISCUSSION

Energy Expenditures for Standing and Lying

Elk calves weighing from 29.0 to 75.0 kg ($\bar{x} \pm$ SD = 49.8 ± 13.9), all less than 4 months of age, expended an average of 0.0362 ± 0.0051 kcal/kg/min for standing ($N = 21$) and 0.0289 ± 0.0049 kcal/kg/min for lying ($N = 31$). This energetic increment of 25% between postures is similar to values reported for other ungulates, which range from 21 to 37% ($\bar{x} = 28 \pm 7\%$) for elk, moose (*Alces alces*), roe deer (*Capreolus capreolus*), and pronghorn (*Antilocapra americana*) (Wesley et al. 1973, Weiner 1977, Gates and Hudson 1978, Renecker et al. 1978). If the animals in the current study had been fasted and the lying metabolic rates were equal to the interspecific norm (Kleiber 1975), the caloric increment of standing over lying would have been 40%. Values of 62–63% for white-tailed deer (*Odocoileus virginianus*) (Mattfeld 1974, Mautz and Fair 1980) and 72% for mule deer (Kautz et al. 1982) appear excessively high and may reflect the peculiarities of one animal (Mautz and Fair 1980) or the difficulties in attempting to segregate energy expenditures for different activities in trials

composed of two or more activities (Kautz et al. 1982). An average increment of 28% is approximately three times higher than the 9% suggested as a standard by Moen (1973:348), based on the work of Brody (1945) and others for man and domestic animals, and the 9.7% experimentally determined for caribou (*Rangifer tarandus*) (White and Yousef 1977). The much higher value for wild cervids may result from anatomical differences (Gates and Hudson 1978), an increased alertness while standing, or additional extraneous movements (e.g., head and neck movements) relative to that of domestic ungulates. Attempts to determine the energy expenditure for lying in mule deer fawns were unsuccessful as they virtually refused to recline in the presence of the investigator.

Horizontal and Vertical Locomotion

Energy costs (kcal/kg/min) of horizontal and vertical locomotion for mule deer and elk increased with increasing velocity of travel. In general, there is a linear relationship between oxygen uptake and running velocity. Hoyt and Taylor (1981), however, reported an energetically optimal velocity for each gait in horses, resulting in a relationship for horizontal locomotion best expressed by a series of curvilinear functions. This phenomenon was occasionally seen in elk calves for which all measurements were made consecutively within a given day (Fig. 1). However, all variability in data collection must essentially be eliminated for this relationship to be substantiated. Because the curvilinearity is extremely slight and variability is not easily controlled in field studies using wild ungulates, it is probably more appropriate for most ecological applications to use a linear function between energy expenditure and velocity of travel.

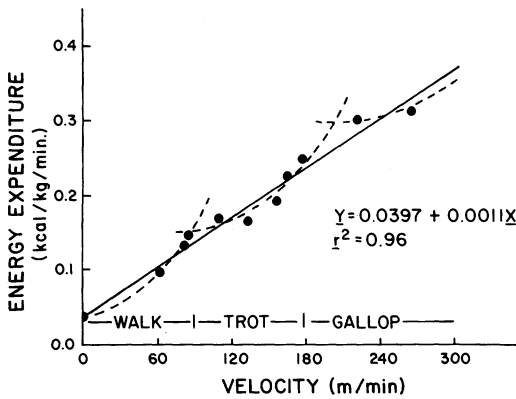The net energy cost of horizontal loco-

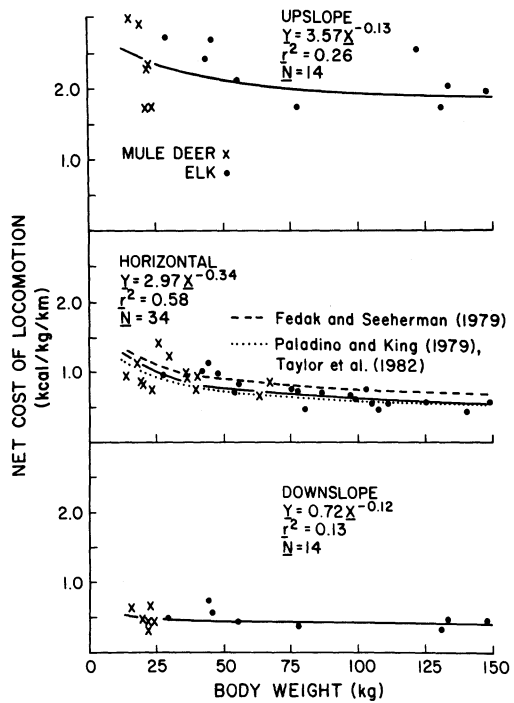Fig. 1. The energetic cost of differing gaits for a 42-kg elk calf.

Fig. 2. The net cost of upslope, horizontal, and downslope locomotion as a function of body weight for mule deer and elk. Energy expenditures for horizontal movement are compared with interspecific regressions for birds including waddlers, mammals, and lizards ($Y = 2.71X^{-0.28}$ [Fedak and Seeherman 1979]; $Y = 2.65X^{-0.32}$ [Paladino and King 1979]; $Y = 2.57X^{-0.32}$ [Taylor et al. 1982]). The lines generated from the two latter equations are not discernibly different and are, therefore, represented by one line.

motion (i.e., the slope of the line relating energy expenditure to velocity of travel) decreases exponentially with increasing body weight for mule deer and elk (Fig. 2). Even though the body weights of these two species do not completely overlap, analysis of variance yielded no difference ($F_{2,30} = 2.52$, $P \simeq 0.10$) between a common relationship and those generated for mule deer and elk individually. The net costs of locomotion for red deer (*Cervus elaphus*) weighing an average of 68.3 kg (0.61 kcal/kg/km) (Brockway and Gessaman 1977), caribou weighing 92.8 kg (0.45 kcal/kg/km) (White and Yousef 1977), and elk weighing 157.0 kg (0.37 kcal/kg/km) (Gates and Hudson 1978) are less than in this study. However, the regression for elk and deer is below the interspecific regression of Fedak and Seeherman (1979), which includes the waddling birds, and above, although not significantly, the interspecific regressions of Paladino and King (1979) and Taylor et al. (1982), which do not include waddlers (Fig. 2).

Relative to horizontal costs, energy expenditures by mule deer and elk increased for upslope travel and decreased to a lesser extent for downhill locomotion (Fig. 2). The average costs of lifting a ki-

logram 1 vertical meter for mule deer (5.99 kcal/m) and elk (5.73 kcal/m) are similar to those of other ungulates, which range from 5.13 kcal/m for red deer to 6.36 kcal/m for sheep (Clapperton 1964, Brockway and Gessaman 1977, Ribeiro et al. 1977, White and Yousef 1977). Neither body weight nor species appear to affect the vertical cost, with the mean cost being 5.93 ± 0.45 kcal/vertical meter for wild and domestic ungulates.

The efficiency of uphill locomotion, calculated as in Taylor et al. (1972), ranged from 28 to 69% ($\bar{x} = 45\%$) for mule deer (14–24 kg) and 36 to 56% ($\bar{x} = 40\%$) for elk (28–145 kg), with no apparent differ-

ence in relation to body weight. Variation in energy expenditure for locomotion uphill by mule deer may reflect the difficulties in working with these animals, actual differences between subject animals, or the fact that the net energy cost increases dramatically at lower body weights. Mean efficiencies of uphill locomotion for wild and domestic ungulates average 43.8 ± 9% (Clapperton 1964, Yousef et al. 1972, Brockway and Gessaman 1977, Ribeiro et al. 1977, White and Yousef 1977, current study). However, upslope efficiencies within a species appear to decline with increasing steepness of the terrain (Yousef et al. 1972, Brockway and Gessaman 1977, White and Yousef 1977).

The amount of potential energy recovered in moving downhill for mule deer and elk decreased with increasing body weight. Downslope efficiencies must decline as the net cost of horizontal locomotion decreases in larger animals while the cost of downhill travel assumes a relatively asymptotic or constant value with increasing body size (Fig. 2). Downhill efficiencies (energy recovered/mechanical energy stored) ranged from 87% for a 25-kg animal to 25% for a 150-kg animal. While others have reported decreasing efficiency with increasingly steep slopes (Margaria et al. 1963, Yousef et al. 1972, Raab et al. 1976, White and Yousef 1977, Cohen et al. 1978), species-specific data that would aid in explaining the relation of downslope efficiency to body weight are not available for comparative purposes. Therefore, reasons why this efficiency should decline with increasing body weight in mule deer and elk are speculative. Intuitively, it would seem that it costs more for a larger long-legged animal to decelerate a larger mass when moving downhill than it would cost a smaller animal.
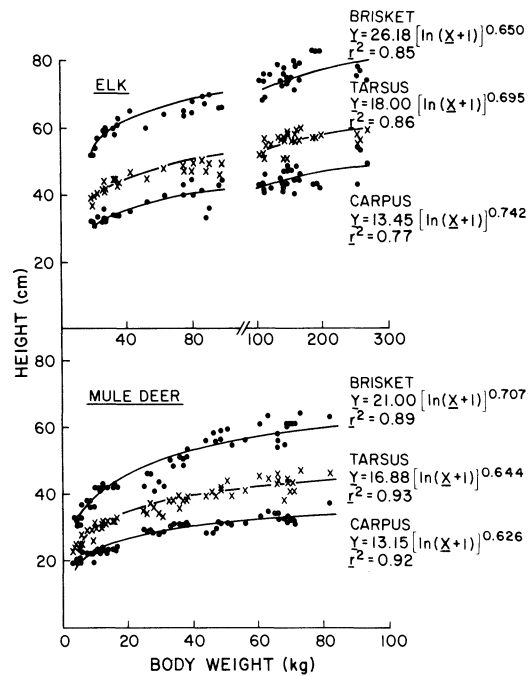

Fig. 3. Brisket, tarsus, and carpus heights as a function of body weight for mule deer and elk.

Locomotion in Snow

Snow cover is a major factor influencing the survival of wintering ungulates because it affects their ability to escape predation, the timing and magnitude of migratory movements, and habitat selection (Edwards 1956; Pruitt 1959; Gilbert et al. 1970; Telfer 1970, 1978; Coady 1974; Prescott 1974; Leege and Hickey 1977; Harestad 1979). Snow impedes movement, increases energy expenditure, and reduces forage availability. While three basic properties of snow—depth, density, and hardness—influence wintering ungulate populations (Coady 1974), snow depth has been considered the most important attribute affecting ungulate movement and mobility (Wallmo and Gill 1971, Hugie 1973, Telfer 1978). Relative to locomotion and energy expenditure, the depth to which an animal sinks in snow is the
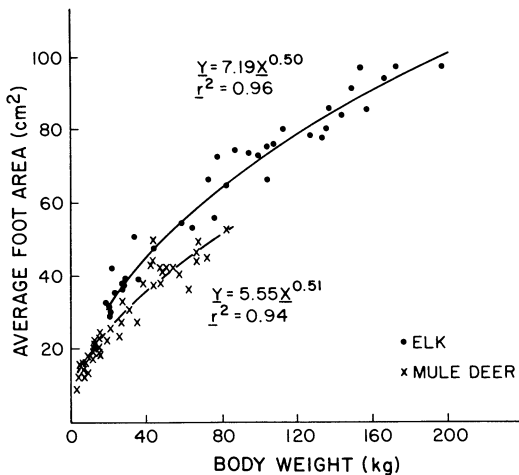
Fig. 4. Average foot area (mean total area of both back and front feet) as a function of body weight for mule deer and elk.

most appropriate measure of "effective" snow depth (Verme 1968).

To assess the ability of mule deer and elk to cope with snow of different depths, the morphological variables of brisket, tarsus, and carpus height were examined as a function of body weight. All three variables approached asymptotic levels at lower heights for mule deer than for elk (Fig. 3). The large variation noted in the function for elk carpus height reflects experimental difficulties in determining midjoint height of a relatively large animal and probably is not an indication of extreme differences between animals.

Others have compared brisket height to body weight for elk (Kelsall and Telfer 1971), white-tailed deer (Kelsall 1969), and Sitka black-tailed deer (*O. h. sitkensis*) (D. E. Spalinger, unpubl. rep., U.S. For. Serv., For. Sci. Lab., Juneau, Alaska, 1981). Values for all three species are greater than those predicted by our equations and suggest an overestimation of true standing height as a result of measurements made from tip of the front hoof to the brisket on dead animals. Brisket height values ob-

tained from prone adult female elk in this study averaged 13 ± 2% higher than measurements made on the same animals while standing. Furthermore, variations from values predicted by our equation may be inherent in the live weight estimates from field-dressed animals for white-tailed deer. Even greater differences were found between predicted values and those observed for Sitka black-tailed deer, however, indicating that these animals may actually have relatively longer legs than their southern counterparts.

Average foot area was less and foot loading greater for mule deer than for elk at similar body weights (Figs. 4, 5). The variation in these functions reflects differences between sexes as well as seasonal weight changes. In heavy snowfall areas where snow depth is greater than sinking depth, mule deer should sink deeper than elk of similar weights. However, in comparing animals of the same age, the average-sized mule deer has a lighter foot loading than does the average-sized elk. For example, a 35-kg mule deer at 6 months of age has a foot loading of 0.26 kg/cm² compared with the 100-kg, 6-month-old elk with a foot loading of 0.35 kg/cm². This interpretation agrees with that of Telfer and Kelsall (1979), who have shown that foot loadings based on specific age-classes for white-tailed deer are lighter than those of elk.

Foot loadings for captive mule deer and elk were lower than values obtained by Telfer and Kelsall (1979) and Kelsall and Telfer (1971) for dead elk and white-tailed deer. This discrepancy may result from differences in the method of measurement. The weight of live animals bearing down on the foot effectively enhances foot area, thereby decreasing foot loading. Even though Telfer and Kelsall attempted to simulate the foot postures of the living animal, an underestimation of foot area

would explain their higher foot loading values. Conversely, relatively light foot loading values for captive animals could result from excessive hoof growth. However, we attempted to minimize this occurrence by maintaining animals periodically on concrete or rock floors and by trimming the hooves of those animals in outdoor pens.

Foot loading is only an index. In combination with the forces of momentum, the distribution of body weight on two or three feet during locomotion (walk vs. trot) increases the foot loading of the animal. On the contrary, the ability of the animal to spread the toes voluntarily and reduce the phalange to ground angle when walking on soft surfaces provides some compensation. Mule deer are particularly adept at collapsing the phalanx to increase the area of the foot, thereby decreasing foot loading and hence sinking depth. Elk seem almost incapable of this behavior.

Elk calves and mule deer fawns may be more restricted than adults of the same species in their movement in deep snow areas because of shorter leg length. In general, the legs of young ungulates during the first winter are approximately 10% shorter than those of adults (Kelsall 1969, Kelsall and Telfer 1971, Telfer and Kelsall 1979, current study). Partial compensation for this disadvantage is that their legs are proportionately longer and foot area is larger relative to body weight. From an interspecific standpoint, mule deer also possess proportionately longer legs and a larger foot area than do elk of similar age.

The energetic costs of travel in snow for mule deer and elk are influenced by the velocity at which the animal travels, the depth to which it sinks, and the density of the snow. All animals in this study sank entirely to the ground, i.e., sinking depth equaled snow depth. Thus, snow hardness, or the capacity of the snow to support the
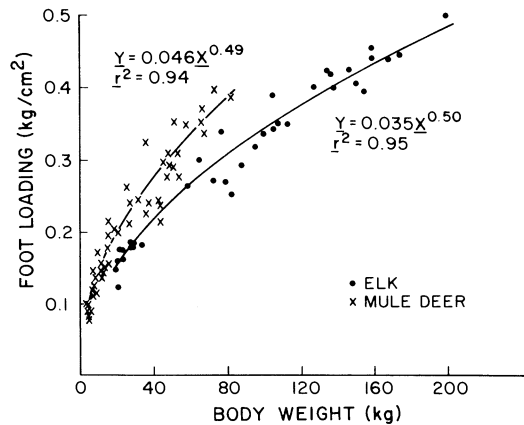

Fig. 5. Foot load as a function of body weight for mule deer and elk.

animal, was not measured even though it may be critically important in other areas.

Energy expenditures (kcal/kg/min) by both mule deer and elk increased with velocity of travel and sinking depth (Figs. 6, 7), as reported by Mattfeld (1974) for white-tailed deer and Heinonen et al. (1959) and Ramaswamy et al. (1966) for humans. Because of the similarity in intercepts, individual regressions between the velocity of travel and energy expenditure can be compared by slope values (Fig. 6). For example, the net energy cost of travel for a 100-kg elk calf in 58 cm of snow is approximately five times the cost of locomotion without snow. This increase in energy expenditure as a function of snow depth may be the result of a reduction in the ballistic movements of the legs, an increase in the height to which the feet must be lifted (Heinonen et al. 1959), or an increase in the swinging motion of the body (Ramaswamy et al. 1966). By voluntarily decreasing the velocity of walking as snow depth increases (Heinonen et al. 1959, Ramaswamy et al. 1966, Mattfeld 1974), free-ranging ungulates maintain energy expenditures at acceptable levels.
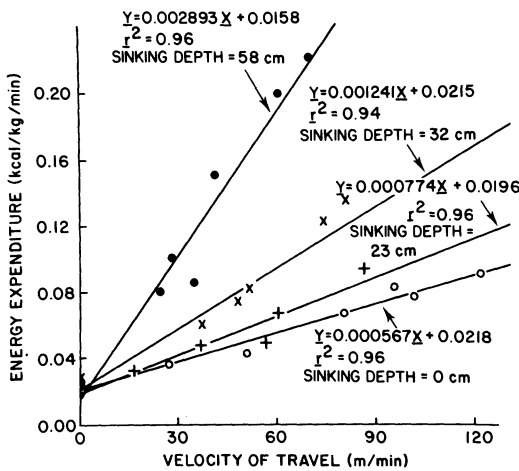
Fig. 6. The energetic cost of locomotion in snow of varying depths as a function of velocity of travel for a 100-kg elk calf. Snow density = 0.2 g/cm³.

Fig. 7. The relative increase in the net cost of locomotion in snow of two different densities (large symbols = 0.4, small symbols = 0.2 g/cm³) as a percentage above the cost of travel without snow as a function of relative sinking depth for mule deer and elk. Dashed line represents a similar function for white-tailed deer (Mattfeld 1974). The larger equation predicts the relative increase in energy expenditure (Y) for locomotion in snow of a given density (ρ) and relative sinking depth (X).

The relative increase in net energy expenditure as a percentage above the cost of travel without snow increased exponentially as a function of relative sinking depth (Fig. 7). Relative sinking depth, or the height on the leg to which the animal sinks as a percentage of its brisket height, facilitates the comparison of energy costs for two morphologically similar species of different sizes. There is no apparent difference in the increased energy expenditures by elk and deer as they move through snow of the same relative sinking depth.

Energy expenditure for locomotion in snow by mule deer and elk increased with increasing snow density (Fig. 7). Oxygen use values in wet snow (snow density = 0.4 g/cm³) were elevated ($F_{2,22} = 49.5$, $P < 0.001$) from powdery snow (snow density = 0.2 g/cm³). Heavier snow presumably inhibits locomotion by increasing drag on the legs or body (Coady 1974) and may also reduce the capability of the animal to travel by wading, as in powdery snow, and necessitate lifting the legs to higher levels.

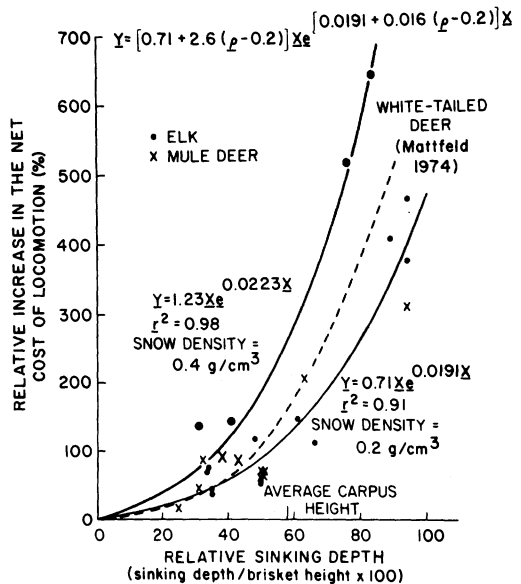The average carpus height for mule deer and elk is approximately 58% of bris-

ket height. While this is not the point of maximum curvature for either relationship shown, energy costs of locomotion are dramatically elevated in snow depths above front knee height. Although all measurements of locomotion in snow were obtained from areas of uniform snow quality in depths less than brisket height, several metabolic values were collected from snowfields in which the animals periodically broke through snow crusts and in areas where snow depths exceeded brisket height. In both situations, energy expenditures were substantially increased. Hepburn (1959) and Mattfeld (1974) also concluded that breakable crusts impede travel and exaggerate energy costs. For sinking depths greater than brisket height, mule deer and elk resorted to exaggerated bounding gaits that greatly increased en-

ergy expenditures because of vertical displacement of the entire body mass.

The equation that predicts the relative increase in the net cost of locomotion in a given snow density and depth (Fig. 7) assumes a linear function for densities only between 0.2 and 0.4 g/cm³. These values, nevertheless, are average snow densities for new-fallen and settled snows, excluding crusted and wind-packed areas (U.S. Army Corps Eng. 1956, Keeler and Weeks 1967, Billello et al. 1970, Fitzharris 1975). Without regard to geographical region, snow densities generally range from slightly less than 0.1 to 0.6 g/cm³.

Thus, when moving through powdery snow where sinking depth equals snow depth, increments of energy expenditure in mule deer are higher than in elk. Relative sinking depth is greater for the shorter legged deer than for an elk of similar age. However, in dense snow where sinking depth is proportional to foot loading, increments of energy expenditure in deer relative to elk of a similar age would be less. With their lighter foot loading and proportionately longer legs, relative sinking depth for deer is reduced.

The sinking depth of the animal and consequently energy expenditures for locomotion in snow are affected by three factors related to the animal—foot loading, leg length, and velocity—and three snow characteristics—depth, density, and hardness. Because data for this study were collected only in regions where mule deer and elk sank entirely to the ground, the effects of foot loading, velocity of travel, and snow hardness on sinking depth could not be analyzed. The equation predicting the relative increase in the net cost of locomotion (Fig. 7), however, does encompass snow density and depth and is directly related morphologically to the animal via brisket height. Factors other than snow density, including snow temperature, form and size of the snow crystals, and hardness of subsurface crusts are also relevant to the sinking depth of an animal (Kelsall and Prescott 1971). Snowfields encountered by mule deer and elk are not always uniform. Nevertheless, this equation does provide a minimum estimate of the energy expenditures for locomotion in snow by mule deer and elk and serves as a baseline for further studies.

The migratory movements of large herds of ungulates are probably determined in part by the interaction of the animal's morphology and existing snow conditions. Although elk have been observed to travel with relatively little difficulty in powdery snows as deep as 102 cm (Gaffney 1941), free-ranging herds are generally restricted in distribution by snow depths greater than 46 cm (Beall 1974, Leege and Hickey 1977, Adams 1982). Snow depths of 51 and 122 cm have been reported as critical depths for deer because of greater energy expenditures and reduced food supplies (Severinghaus 1947, Leopold et al. 1951). However, average snow depths beyond 25 cm are sufficient to discourage occupation of a given area by deer and are associated with initiation of deer movement to winter habitat (Kelsall and Prescott 1971, Wallmo and Gill 1971).

Assuming that body weight averages 265.8 kg in adult elk (Skinner 1946, Murie 1951, Quimby and Johnson 1951, Cowan and Guiguet 1956, Greer and Howe 1964, Blood and Lovaas 1966) and 66.5 kg in adult mule deer (Anderson et al. 1974), brisket heights for these animals would be approximately 80.1 and 58.0 cm, respectively. Relative sinking depths for the above adult animals would be 57.4 and 43.1%, assuming the previous snow depths (46 and 25 cm) which induce movement of elk and deer to more favorable habitats. A profound increase in energy expendi-

ture, even in low density snows, clearly occurs beyond this range of relative sinking depths (Fig. 7). Hence, while recognizing that such alteration in the use of habitat is also a function of forage availability, the significant increase in the net cost of travel in snow depths greater than 46 cm for elk and 25 cm for deer verifies, from an energetic standpoint, the preceding field observations.

The energetics of locomotion in snow are particularly important in high-use recreation regions, where increased human visitation may induce animal flight causing increased energy expenditures. The nature and intensity of these reactions are influenced by weather conditions, including snow depth and sinking depth, cover type and distribution of vegetation, topography, individual species behavior and sensitivity, and the spatial or temporal distribution of human disturbance (Richens and Lavigne 1978, Aune 1981). Flight distances decline from early to late winter as the animals become habituated and as body energy reserves are depleted. Greater flight distances occur in response to skiers or individuals on foot than to snowmobiles, suggesting that the most detrimental disturbance to the wintering animal is that which is unanticipated (Richens and Lavigne 1978, Aune 1981). Flight distances attributed to snowmobile disturbance in Yellowstone National Park averaged 33.8 m for elk and 28.6 m for mule deer, in comparison with those arising from skier interactions averaging 53.5 m for elk and 52.4 m for mule deer (Aune 1981).

Based on Figs. 6 and 7, energy expenditure for locomotion in snow per unit distance was calculated as a function of velocity of travel for average adult elk and mule deer (Fig. 8). The cost of transport decreased with increasing speed and assumed a relatively asymptotic or optimal value at the same velocity for all snow depths. An energetic cost was then estimated for the response of wintering ungulates to human recreational activities from the above observations. Additional net energy expenditures per disturbance ranged from 4.9 to 36.0 kcal in elk and 2.0 to 14.7 kcal in deer, depending on flight distance and a fivefold variation in the cost of locomotion at the optimal velocity in snows of different depths. Assuming a gross energy coefficient of 4.4 kcal/g, a digestible energy coefficient of 0.45 (Hobbs et al. 1981), a metabolizable energy coefficient of 0.82, and a net energy coefficient of 0.70 for winter range forage, these energy expenditures are roughly equivalent to the necessary additional consumption of 4.3–31.7 g of forage dry matter by elk and 1.8–12.9 g by mule deer, if the requirement is to be met by foraging.

Locomotion Through Slash

Logging slash is an important agent restricting animal use of logged areas (Wallmo 1969, Wallmo and Schoen 1980). Slash depth in excess of 0.5 m substantially suppresses elk and deer use of these openings (Lyon 1976, Lyon and Jensen 1980). While snow may alter the effects of slash by decreasing forage availability and increasing energy costs as a function of depth, or by actually reducing the amount of slash relative to snow crusts which provide support to animals, the energetic cost of locomotion through slash during snow-free periods was estimated (Fig. 9).

Several assumptions in this analysis are not always realistic, but support a first approximation of energy expenditure: (1) slash deposition is uniform such that impediments, including logs and branches, are equal in size; (2) between obstacles, the energy cost to the animal is equal to that of horizontal locomotion (Fig. 2); (3)
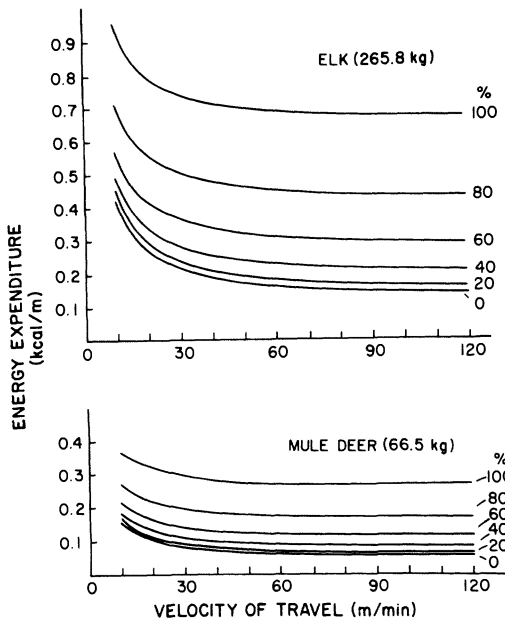
Fig. 8. Energy expenditures of locomotion in snow at six relative sinking depths as a function of velocity of travel for a 248.6-kg elk and a 66.5-kg mule deer.
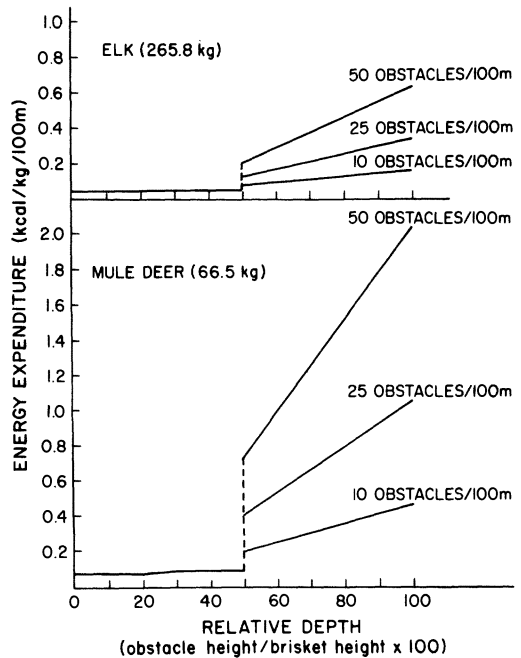

Fig. 9. Predicted energy expenditures of locomotion (i.e., the posture of locomotion plus the net cost) through slash deposits of varying densities as a function of relative depth for a 265.8-kg elk and a 66.5-kg mule deer.

for debris less than 50% of brisket height in diameter, the animal simply lifts its legs higher during travel and oxygen use is similar to that of locomotion in dense snow (Fig. 7); and (4) for debris greater than 50% of brisket height in diameter, the animal jumps over obstacles and energy expenditures are estimated at 5.9 kcal/vertical meter. During jumping, animals are assumed to fold their legs up to 50% of brisket height and clear all obstacles by 0.15 m.

The predicted energy cost of locomotion through slash increases as a function of relative depth and obstacle density (Fig. 9). Expenditures per kilogram are greater for the average-sized mule deer (66.5 kg) than for the average elk (265.8 kg) and increase dramatically in both species when jumping becomes necessary. The increase in energy cost for each additional unit of obstacle depth less than 50% of brisket

height is small. Although these expenditures are estimated from the curvilinear function of locomotion in dense snow, only a fraction of all steps taken by the animal during 100 m of travel through slash of the designated densities would encounter an obstacle and, therefore, require additional energy expenditure for lifting the legs. Energy expenditures at these densities are essentially identical. While the obstacle height that induces jumping of animals was estimated at 50% of brisket height for this analysis, subsequent research is necessary to assess the validity of this estimate. Animal stride length relative to the diameter of obstacles may be a more realistic determinant of jumping than is simply the height of the impediment.

This model provides a minimum ener-

gy estimate for direct travel through slash, since costs of locomotion are often compounded by shrub or young tree biomass that may impede travel and foraging efforts. If animals tend to avoid obstacles by meandering, thereby increasing the proportion of horizontal travel and decreasing total energy expenditure by not jumping, the costs estimated by the above model are maximum relative to the expenditures experienced by the animal.

MANAGEMENT IMPLICATIONS

Little can be done to reduce the energetic cost to an animal of a minimum amount of travel through snow. Unnecessary energy expenditures, however, can be limited by minimizing human disturbances. While both the number of animals induced to flee as a result of winter recreationists and the frequency of disturbances vary, the additional energy drain on a wintering ungulate population on poor winter range may be an important factor in its survival. Management should consider restricting human access to ungulate winter use areas if maximum survival of ungulate herds is a primary concern.

Measurements of the energy expenditure for locomotion by wild ungulates provide insight into the effects of forest management on habitat quality. Logging affects energy requirements of elk and deer by influencing snow depth through removal of canopy interception of falling snow. For example, assuming a snow density of 0.3 g/cm^3 and a snow depth of 50 cm in the opening created by a recent clear-cut, snow depth in a conifer forest with 70% canopy closure would be about 5 cm (Harestad and Bunnell 1981). The relative increase in the cost of locomotion (Fig. 7) for a 265.8-kg elk would be 220% in the clear-cut vs. 7% in the forest when compared to snow-free conditions. Similar values for a 66.5-kg deer would be 498% in the clear-cut vs. 10% in the forest.

The slash deposition of logging operations varies as a function of the vegetation type, age of stand, and management operations and has rarely been quantified (Dyrness 1965, Reynolds 1966). The high energetic cost of locomotion for mule deer and elk at high slash densities and depths would clearly be one factor favoring slash avoidance. With a recognition of the energetic demands of different movement patterns, there is need for more intensive and detailed studies of the use of clearcuts by deer and elk within an energetic framework.

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