

RESEARCH ARTICLE

Quantifying energetic costs and defining energy landscapes experienced by grizzly bears

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ABSTRACT

Animal movements are major determinants of energy expenditure and ultimately the cost–benefit of landscape use. Thus, we sought to understand those costs and how grizzly bears (*Ursus arctos*) move in mountainous landscapes. We trained captive grizzly bears to walk on a horizontal treadmill and up and down 10% and 20% slopes. The cost of moving upslope increased linearly with speed and slope angle, and this was more costly than moving horizontally. The cost of downslope travel at slower speeds was greater than the cost of traveling horizontally but appeared to decrease at higher speeds. The most efficient walking speed that minimized cost per unit distance was $1.19 \pm 0.11 \text{ m s}^{-1}$. However, grizzly bears fitted with GPS collars in the Greater Yellowstone Ecosystem moved at an average velocity of $0.61 \pm 0.28 \text{ m s}^{-1}$ and preferred to travel on near-horizontal slopes at twice their occurrence. When traveling uphill or downhill, grizzly bears chose paths across all slopes that were ~54% less steep and costly than the maximum available slope. The net costs ($\text{J kg}^{-1} \text{ m}^{-1}$) of moving horizontally and uphill were the same for grizzly bears, humans and digitigrade carnivores, but those costs were 46% higher than movement costs for ungulates. These movement costs and characteristics of landscape use determined using captive and wild grizzly bears were used to understand the strategies that grizzly bears use for preying on large ungulates and the similarities in travel between people and grizzly bears that might affect the risk of encountering each other on shared landscapes.

KEY WORDS: Energetics, *Ursus arctos*, GPS, Movement ecology, Locomotion, Greater Yellowstone Ecosystem

INTRODUCTION

Energy is a limiting factor for many species of wildlife (Parker et al., 1984; Shepard et al., 2013). Because daily and seasonal movements are major determinants of energy expenditure and balance, quantifying the landscape of energy use allows us to understand the biological and physical constraints acting on animals occupying different environments or pursuing different life strategies (Dunford et al., 2020; Halsey, 2016; Shepard et al., 2013; Wilson et al., 2012). Three key parameters must be quantified to effectively understand the energy

landscape of an animal: (1) the energetic costs of moving at various speeds on differing slopes, (2) the movement behavior of free-ranging animals, using location and activity data, and (3) the physical landscape through which the animal moves (Avgar et al., 2013; Signer et al., 2019; Walker et al., 2015; Wilson et al., 2008, 2006). Use of animal telemetry is widespread and allows us to quantify movement, behavior and resource selection (Boyce et al., 2002; Millsbaugh et al., 2006; Schick et al., 2008; Thurfjell et al., 2014; Winnie and Creel, 2007). However, quantifying energy expenditure from telemetry data is more difficult. Whereas measuring the costs of movement in laboratory conditions is a relatively straightforward and well-defined process (Hoyt and Taylor, 1981; Taylor et al., 1982), applying those costs to movements of wild animals and understanding how those animals view and use the environment is more challenging. Animals can continuously alter their movement paths, travel speed and angle moving up and down slopes (Dunford et al., 2020; Halsey and White, 2017; Shine et al., 2015; Wickler et al., 2000).

Grizzly bears (*Ursus arctos*) occupy diverse habitats and can move vast distances in search of resources and mates, often over rugged and steep terrain. Grizzly bears in the Greater Yellowstone Ecosystem (GYE) have expanded into areas that have been unoccupied for decades (Bjornlie and Haroldson, 2017). Grizzly bears alter their movement patterns and habitat use in response to a wide range of environmental cues, including seasonal food resources, human recreation (e.g. hiking, camping, hunting), livestock grazing and road use (Fortin et al., 2016, 2013; Ordiz et al., 2013; Parsons et al., 2020; Roever et al., 2010; Schwartz et al., 2010; Wilson et al., 2005). With a growing wildland–urban interface and increasing and changing patterns of human recreational use on public land, understanding how large carnivores use those environments can help managers reduce the potential for conflict and aid in land management decisions (Coleman et al., 2013a,b; Dunford et al., 2020; Gunther et al., 2004).

The objectives of our study were to measure energetic costs of grizzly bears moving at various speeds across a range of slope angles and use that information to understand how those costs affect grizzly bear movement patterns in the wild. We hypothesized that grizzly bears select travel speeds and slope angles that optimize their energy expenditure in mountainous terrain. The optimization process for the energetics of travel is defined by a balance between minimizing the cost per unit distance traveled, which often occurs at higher speeds and slope angles, and reducing the cost per unit time, which occurs at lower speeds and slope angles (Birn-Jeffery and Higham, 2014; Halsey, 2016). Grizzly bears are opportunistic omnivores that consume food resources that are often dispersed and patchily distributed. Because traveling and foraging can occur simultaneously and grizzly bears occupy the top of the food chain, they do not need to move fast to reduce exposure to predators. Therefore, we hypothesized that minimizing the cost per unit time by traveling at slower speeds and lower slope angles would be more important to grizzly bears than minimizing the cost per unit distance.

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Finally, grizzly bears are one of the few large plantigrade mammals, like humans, and therefore may have a different cost and efficiency of movement that would affect landscape use in comparison to digitigrade and unguligrade mammals (Pagano et al., 2018; Shine et al., 2015). Pagano et al. (2018) previously concluded that the net cost of walking in grizzly bears and polar bears was 10% higher than that predicted for other quadrupedal mammals. Although multiple factors contribute to the choice of movement paths and speeds, detailed knowledge of the energetic and physiological costs of movement can provide a better understanding of landscape use by grizzly bears. Such insight can help managers assess potential risks due to landscape features that affect interactions between grizzly bears and people.

MATERIALS AND METHODS

Study design

We measured oxygen consumption (\dot{V}_{O_2}) of nine grizzly bears (*Ursus arctos* Linnaeus 1758; Table 1) at the Washington State University Bear Research, Education, and Conservation Center (Pullman, WA, USA) via open-flow respirometry using methods previously described by Pagano et al. (2018). The 2 adult males were wild-caught in the GYE as part of conflict management actions, and the remaining 2 males and 5 females were captive-born, bottle-raised progeny of wild-caught parents. The bears were trained over 2 months and conditioned to rest while lying in sternal recumbency, sit, stand, and walk on a treadmill (T1 Trotter horse treadmill, Horse Gym USA, LLC, Wellington, FL, USA) at various speeds. Travel velocity did not go above a fast walk to ensure the safety of the bears should they suddenly stop at higher speeds. Bear participation in the study was voluntary in that no bear was forced to move on the treadmill. Whenever a bear stopped walking, turned around or in some way indicated that it did not want to participate on a particular day, it was released from the treadmill and returned to its home pen. Body mass was measured weekly to the nearest 0.5 kg using an electronic platform scale. The research was approved by the Animal Care and Use Committees of Washington State University (protocols 04780 and 04952).

The upper animal-containment part of the treadmill was extensively modified from that designed for horses (Fig. 1). A new reinforced steel frame was built to which polycarbonate sheets were attached to the sides, front and top to create a metabolic chamber measuring 2.7 m×0.9 m×1.2 m. Fresh air entered through the bottom of the treadmill and was drawn out from the top. To reduce equilibration time, air was recirculated at 5.7 m³ min⁻¹ using air-tight external tubing that drew air in from the center and exhausted air at both ends of the enclosure via a 10 cm inline bilge blower (Turbo

4000 Series II, Attwood Corporation, Lowell, MI, USA). After the bear entered the treadmill, the back door was rolled shut and latched to create an air-tight seal. The front of the treadmill was fitted with an air-tight feed box in which small food rewards were placed. Personnel responsible for encouraging the bear to move on the treadmill placed their hand into a sealed rubber glove fastened to the inside of the feed box and passed food to the bear through a 4 cm hole. Food intake per session ranged from 2000 to 2800 g. The treadmill was designed to incline up to 10 deg. With additional blocking (Fig. 1), we were able to measure \dot{V}_{O_2} on the horizontal and at positive and negative 10% and 20% slopes (5.7 and 11.3 deg).

Metabolic measurements

We used a vacuum pump (FlowKit Mass Flow Generator – 2000, Sable Systems International, Inc., Las Vegas, NV, USA) to draw air into the treadmill at 700 l min⁻¹ during measurements. We monitored flow rates and maintained oxygen levels at ≥20%. Sub-samples of air from the exhaust port of the chamber were drawn at 175 ml min⁻¹ through a series of six columns filled with desiccant (Drierite, W. A. Hammond Drierite, Xenia, OH, USA) and scrubbed of carbon dioxide (Sodasorb, W. R. Grace & Co, Chicago, IL, USA) before entering the oxygen analyzer (Sable Systems International, Inc.). We monitored percentage oxygen in the expired air continuously and recorded values once per second using Expedata Analysis software (Sable Systems International, Inc.). Air temperature within the chamber ranged from 17.7 to 34.3°C (mean 28.9°C). All measurements were made in the shade, and none of the bears panted or showed any sign of thermal distress. We converted values to \dot{V}_{O_2} using eqn 4B from Withers (1977), assuming a respiratory quotient of 0.78 (Pagano et al., 2018). All values were corrected to standard temperature and pressure, dry, by recording air temperature, atmospheric pressure and relative humidity (RH) at each measurement. Saturated water vapor pressure (SWVP) was calculated from air temperature, water vapor pressure was calculated from SWVP and RH, and flow rates were adjusted for water vapor using eqns 8.6, 14.4 and 14.5 in Lighton (2008). Carbon dioxide concentrations were small enough because of the high flow rate of air through the chamber to be disregarded when adjusting flow rates for water vapor. We calibrated the entire system prior to measurements with dry ambient air (20.95% O₂) and periodically with dry N₂ gas (Fedak et al., 1981).

Measurements of \dot{V}_{O_2} were made over 6–16 min intervals, with at least 5 min of steady-state \dot{V}_{O_2} measurement to ensure equilibration. At least one resting measurement was taken following an overnight fast to ensure a post-absorptive state. We estimated net cost of transport (NCOT) as the slope of the relationship between \dot{V}_{O_2} (ml O₂ kg⁻¹ h⁻¹) and velocity (km h⁻¹) (Taylor et al., 1982) and estimated total cost of transport (COT) as the slope plus y-intercept (postural cost of activity). All values are expressed as a function of each bear's mass at the time of each measurement. We compared the NCOT of grizzly bears with that for humans, mountain lions (*Puma concolor*), dogs (*Canis lupus*) and large ungulates (current study; Dunford et al., 2020; data summary of Halsey and White, 2017; McArdle et al., 2000). We used equations developed by Taylor et al. (1972) to calculate the net energy cost of vertical ascent during uphill locomotion (E_{up}):

$$E_{up} = \frac{(S_{up} - S_{level}) \times 20.1}{\sin \theta}, \quad (1)$$

where E_{up} is the energetic cost (J kg⁻¹) of raising 1 kg one vertical meter, S_{up} is the NCOT (ml O₂ g⁻¹ km⁻¹) for walking uphill at a set

Table 1. Summary of data for captive grizzly bears used in this study

Bear	Sex	Age	Body mass (kg)
John	Male	15	250–265
Frank	Male	15	239–242
Luna	Female	14	161–183
Kio	Female	12	143–154
Peeka	Female	12	139–153
Adak	Male	2	104.0
Dodge	Male	2	126–132
Willow	Female	2	97.0
Zuri	Female	2	91–114

Bears (at the Washington State University Bear Research, Education, and Conservation Center, Pullman, WA, USA) were weighed weekly and body mass for that week was used to calculate mass-specific metabolic rate. Body mass ranges reflect those during treadmill studies.



Fig. 1. The treadmill and its modifications used to measure energy expenditure of grizzly bears while lying, sitting, standing and walking on horizontal and up and down slopes. Both up and down slopes were created by lifting the front or back of the treadmill to the desired angle, and bears were encouraged to walk at a specific speed by providing small food rewards (e.g. apple slices).

gradient, S_{level} is NCOT for horizontal movement ($\text{NCOT}_{\text{horizontal}}$, $\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$), 20.1 is the energy equivalent of oxygen ($\text{J ml}^{-1} \text{ O}_2$), and $\sin\theta$ is the fraction of a vertical meter per meter traveled.

To calculate the net energy cost to descend vertically we used (E_{down}):

$$E_{\text{down}} = \frac{(S_{\text{level}} - S_{\text{down}}) \times 20.1}{\sin\theta}, \quad (2)$$

where E_{down} is the energetic cost (J kg^{-1}) of lowering 1 kg one vertical meter, S_{down} is the NCOT ($\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$) for walking downhill on a constant gradient, S_{level} is $\text{NCOT}_{\text{horizontal}}$ ($\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$), 20.1 is the energy equivalent of oxygen ($\text{J ml}^{-1} \text{ O}_2$), and $\sin\theta$ is the fraction of a vertical meter per horizontal meter traveled.

Quantifying movement and estimating energy expenditure by wild bears

We applied the energetic measurements made using the captive bears to movements of grizzly bears in the GYE using equations for uphill and downhill travel. Grizzly bears occupy $>68,000 \text{ km}^2$ in the GYE, which consists of a high-elevation plateau surrounded by 14 mountain ranges with elevations $>2130 \text{ m}$ and contains the headwaters of three continental-scale rivers. Lower elevations ($<1900 \text{ m}$) are characterized by grasslands or shrub steppes. Forest communities dominate elevations above 1900 m , with the upper tree line around 2900 m . Alpine tundra occurs at the highest reaches of all major mountain ranges.

We used GPS data ($n=64,059$ locations) from 30 grizzly bears (24 males, 6 females, ranging in age from 3 to 15 years old) captured and fitted with GPS telemetry transmitters (Telonics, Mesa, AZ, USA) during 2004–2017. Capture and handling of grizzly bears was conducted using methods developed by Blanchard (1983) and Schwartz et al. (2006) and conformed to the Animal Welfare Act and to US Government principles for the use and care of vertebrate

animals used in testing, research and training (US Geological Survey Animal Care and Use Committee protocol #201201). Captures were conducted under US Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40(b)], with additional state research permits for Wyoming, Montana and Idaho, and National Park Service research permits for Yellowstone and Grand Teton national parks. We used GPS data from the downloaded, on-board memory after collar retrieval, irrespective of transmitter type. We excluded three-dimensional and two-dimensional GPS fixes with position dilution of precision (PDOP) >10 (D'Eon and Delporte, 2005). Additionally, we excluded fixes collected during the typical denning months of December–April. Julian dates for GPS data ranged from 87 to 353 with an average of 57.6 monitoring days per bear. Fix intervals of GPS locations ranged from 13 to 208 min. Because much of the movement data that we used came from bears wearing GPS collars with longer fix intervals, we corrected those movement rates to what would have occurred if all bears were wearing collars with a 13 min fix interval. This was done by using a subset of the 13 min collar data that met the following criteria to ensure as much as possible that we were measuring travel speed: (1) movement distances were $>50 \text{ m}$ for each 13 min step, (2) each 208 min step was complete, and (3) for every track there were at least two consecutive, complete 208 min steps. Once those tracks were identified, we started with the 13 min locations and dropped every other GPS location to get 26 min fix locations, 52 min locations and ultimately 208 min locations to determine velocity of travel as fix intervals became longer (Dewhirst et al., 2016; Pépin et al., 2004; Rowcliffe et al., 2012) (Fig. 2). We then used the equation from Fig. 2 relating fix interval to velocity to correct all travel speeds to our shortest fix interval of 13 min for further analysis.

We grouped GYE grizzly bear data by fix interval (e.g. 13, 26, 52 min) and used the `crawlwrap` function from package `momentHMM` (McClintock and Michelot, 2018) in R (<http://www.R-project.org/>) to perform a continuous time-correlated random walk

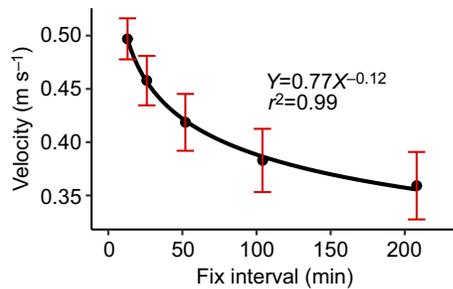


Fig. 2. Relationship between mean velocity of travel and fix interval of GPS collars worn by grizzly bears in the Greater Yellowstone Ecosystem. Data were used to estimate bias and correct movement rates to 13 min intervals for bears wearing GPS collars with fix intervals longer than 13 min. Because of the sinuosity of most travel paths, shorter fix intervals identifying more locations along the path led to longer travel distances per unit time and, therefore, higher velocities of travel. Error bars show standard error of the mean velocity among individual bears for each fix interval.

(CRAWL) model to predict locations based on fix interval and GPS locations. Next, we used package *adehabitatLT* (<https://www.faulnia.it/animove/trac>) to convert steps to *ltraj* objects and subset to each step to 100 m intervals using the *redistraj* function and converted back to a dataframe using the *ld* function. We used dx , dy and dt variables from the *redistraj* function to calculate stop coordinates and step time intervals. We extracted elevation at start and stop points from a 10 m DEM (National Elevation Dataset, USGS, EROS Data Center) and used the difference between the points divided by the step distance multiplied by 100 to calculate percent slope for each 100 m step. We used path distance and time interval between steps to calculate velocity. Percent slope was extracted at the start coordinate for each 100 m step to represent the gradient available to the bear at each step. To estimate total cost of transport, we developed two continuous scale equations (uphill and downhill) by regressing the gradients used in the treadmill studies (i.e. 0%, 10% and 20%) to the slopes of the equations describing COT (Fig. 3A). Slopes for each 100 m grizzly bear movement were calculated using the change in elevation divided by horizontal distance multiplied by 100. Thus, total cost of uphill and horizontal movement (COT, $J kg^{-1}$) was calculated for each animal and step using the following equation:

$$COT_{\text{uphill}} = \{[(0.4091 \times S) + 2.2853] + I\} \times v \times D, \quad (3)$$

where S is percent slope traveled multiplied by 100, v is the velocity in $m s^{-1}$, I is the intercept ($2.835 J kg^{-1} s^{-1}$) for uphill travel, and D is the duration of a step in seconds between GPS locations. The equation for calculating energy expenditure ($J kg^{-1}$) for downhill travel developed from the polynomial regressions of Fig. 3A is:

$$COT_{\text{downhill}} = \{[(0.2000 \times S) - 0.1611] \times v^2\} + \{[(-0.1803 \times S) + 2.6102] \times v\} + I \times D, \quad (4)$$

where S is percent slope traveled multiplied by 100, v is the velocity in $m s^{-1}$, I is the intercept ($2.702 J kg^{-1} s^{-1}$) for downhill travel, and D is the duration of a step in seconds between GPS locations.

To assess whether bears selected for specific gradients, we used ArcMap (ArcMap 10.6.1, Esri, Redlands, CA, USA) to create a 1 km buffer around each track and joined them into a single layer, and extracted random locations from within the 1 km buffer layer ($n=240,000$) and throughout the entire study area ($n=90,000$) to compare with gradients used by bears. We used each bear's travel velocity and slope angle for each 100 m step to estimate its total energy expenditure for that movement based on equations relating

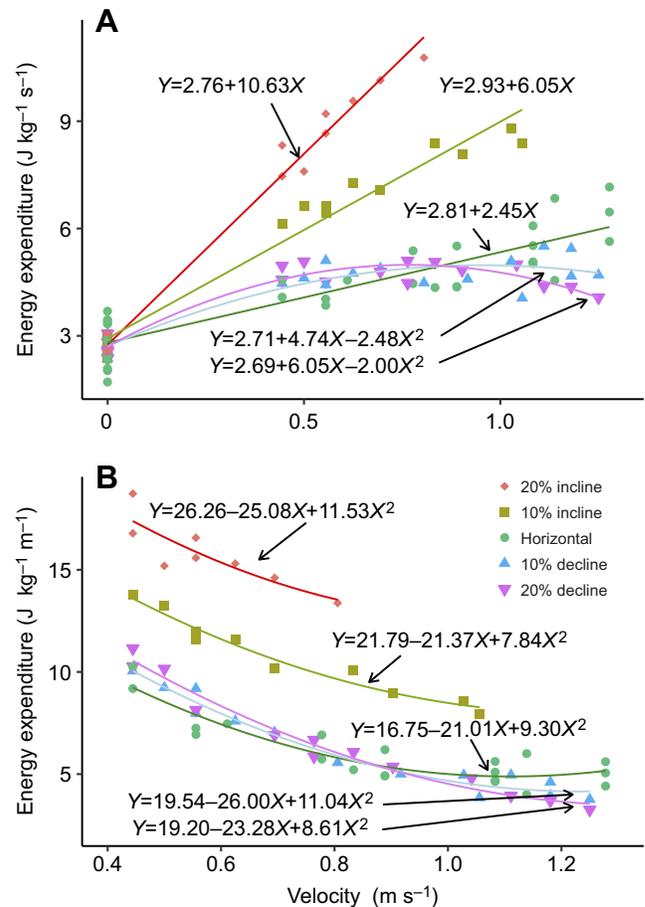


Fig. 3. Relationships between velocity of movement and energy expenditure for captive grizzly bears resting and walking on a treadmill. (A) Cost per unit time. (B) Cost per unit distance. Each data point is the metabolic cost measured for one animal at that speed.

the total cost of movement to velocity and slope angle determined with the captive bears. We also compared maximum metabolic rate measured on the captive bears with those estimated for wild bears traveling at the fastest rate on the steepest slopes by using the 95th percentile values to omit those values that were not physiologically realistic (i.e. caused by unique terrain and travel speed combinations created by subsetting movement steps).

Statistical analyses

We used general linear mixed (GLM) models to evaluate the relationship between metabolic rate and speed. Bear ID was included as a random factor. We used analysis of covariance (ANCOVA) to evaluate whether the relationships between metabolic rate and speed differed between horizontal and uphill slopes and horizontal and downhill slopes and whether there were significant covariate interactions from bear mass. We used ANOVA to test for differences in means for resting metabolic rate and used Tukey's HSD test to test for differences between resting postures. We used a 2-way ANOVA to test for differences in (1) mean horizontal NCOT by locomotion type (i.e. digitigrade, plantigrade and unguligrade) and species and (2) NCOT by locomotion type and species for animals moving on various horizontal and uphill slopes. We used ANCOVA to test for differences in NCOT by gradient and mass for ungulates and carnivores (plantigrade and digitigrade). Species was used as a random factor for NCOT comparisons. All

analyses were conducted in R (<http://www.R-project.org/>). Residuals of each model were examined for normality using $Q-Q$ plots.

RESULTS

Metabolic rate determined on the treadmill

Resting metabolic rate (i.e. lying, sitting or standing) for the captive grizzly bears ranged from 1.71 to 3.69 $\text{J kg}^{-1} \text{s}^{-1}$ and averaged $3.09 \pm 0.62 \text{ J kg}^{-1} \text{s}^{-1}$ (mean \pm s.e.m., $n=9$). Means for resting activity differed (ANOVA, $F_{2,31}=15.36$, $P<0.001$), with both standing ($3.67 \pm 0.41 \text{ J kg}^{-1} \text{s}^{-1}$, $n=8$) and sitting ($3.64 \pm 0.63 \text{ J kg}^{-1} \text{s}^{-1}$, $n=5$), which did not differ from each other ($P=0.993$), being 31% more costly than lying ($2.79 \pm 0.49 \text{ J kg}^{-1} \text{s}^{-1}$, $n=9$) (Tukey's HSD, $P<0.001$). Lying metabolic rate of the grizzly bears was 2.2 times greater than polar bear (*Ursus maritimus*) lying metabolic rate ($1.28 \pm 0.11 \text{ J kg}^{-1} \text{s}^{-1}$, $n=5$) measured on the same treadmill (Pagano et al., 2018). However, when compared with the very calm polar bears, the grizzly bears were constantly fidgeting, with head and leg movements during the measurements, such that there is unlikely to be any significant biological difference in the lying metabolic rates of the two species.

The lack of measurements slower than 0.44 m s^{-1} on all slopes occurred because the bears would not walk consistently for >5 min at slower speeds (Fig. 3). They often either did an awkward sit-crawl at the slowest speeds or demanded more food by pounding at the food bin with their front paws while walking at slightly faster speeds. These behaviors did not occur above 0.44 m s^{-1} . Grizzly bear metabolic rate per unit time while walking on horizontal and 10% and 20% incline gradients increased linearly with velocity (Fig. 3A). There was no significant interaction between speed and bear mass ($F_{6,4}=2.34$, $P=0.215$) on the energy expenditure of bears moving horizontally. Walking on the two upslope gradients was more costly than moving on the horizontal ($F_{2,60}=59.93$, $P<0.001$). There was a significant interaction between speed and gradient on

energy expenditure for uphill and horizontal travel ($\chi^2=72.22$, $P<0.001$). None of the bears were willing to walk on the upslope gradients as fast as they did on the horizontal, with the maximum expenditure ($10.6 \text{ J kg}^{-1} \text{s}^{-1}$, 20% incline) peaking at ~ 5 times the cost of resting. The cost of raising 1 kg by one vertical meter was 35 J on the 10% slope and 41 J on the 20% slope for metabolic efficiencies of 24% and 28%, respectively.

Metabolic rate per unit time on the two downhill slopes relative to velocity was best expressed by curvilinear functions (Fig. 3A). Downhill locomotion was costlier than horizontal movement at slow speeds but became more efficient and less costly at higher speeds. We also fitted linear regressions to the downhill gradient data to determine statistical significance and to compare with other studies that used linear expressions. There was no significant interaction between speed and gradient on energy expenditure ($\text{J kg}^{-1} \text{s}^{-1}$) for downhill travel ($\chi^2=1.88$, $P=0.391$). Metabolic rate per unit distance decreased with increasing speed (Fig. 3B). The most efficient walking speed per unit distance across all slopes (i.e. the minimum asymptote of the lines in Fig. 3B) was $1.19 \pm 0.11 \text{ m s}^{-1}$ (range: 1.08–1.36 m s^{-1}).

The net cost per unit distance traveled by grizzly bears and humans horizontally or uphill did not differ (Fig. 4; $F_{1,2}<0.01$, $P=0.823$), and also did not differ from those of large digitigrade carnivores, such as wolves and mountain lions ($F_{1,6}=0.28$, $P=0.617$). However, movement costs for both plantigrade and digitigrade species were $\sim 46\%$ higher than similar costs for ungulates ($F_{1,16}=10.37$, $P<0.001$). There was no significant difference between species ($F_{5,1}=0.34$, $P=0.190$) or with individual mass ($F_{1,8}=0.01$, $P=0.981$) for ungulates.

Movement characteristics of GYE grizzly bears

The distribution of gradients sampled between the 1 km buffer around each bear's track and the general study area was similar (Fig. 5B). However, bears preferred to travel on near-horizontal

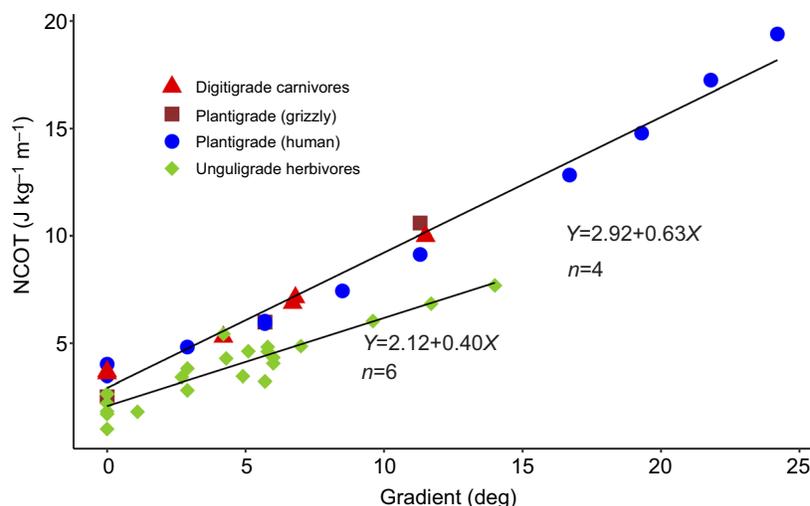


Fig. 4. Net cost of horizontal and uphill movement for large ungulates, digitigrade predators and plantigrades. Net cost of transport (NCOT) is shown for large ungulates: burro (*Equus asinus*), caribou and reindeer (*Rangifer tarandus*), cattle (*Bos taurus*), domestic sheep (*Ovis aries*), elk and red deer (*Cervus canadensis*), and horses (*E. caballus*); digitigrade predators: mountain lion and dog; and plantigrades: grizzly bear and humans (current study; Dunford et al., 2020; Minetti et al., 2002; data summary of Halsey and White, 2017). One of the regressions is for digitigrade and plantigrade mammals combined (i.e. wolves, mountain lions, grizzly bears and humans), and the other is for all ungulates. We did not include data for bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) (Dailey and Hobbs, 1989), which are well above all other animals and may either represent specializations for climbing extremely vertical terrain or reflect difficulty in measuring energetics in that study. Similarly, the values for African lions (Chassin et al., 1976) were not included because their costs did not increase linearly with speed and are markedly different from more recent mountain lion values (Dunford et al., 2020; Taylor et al., 1982; Williams et al., 2014).

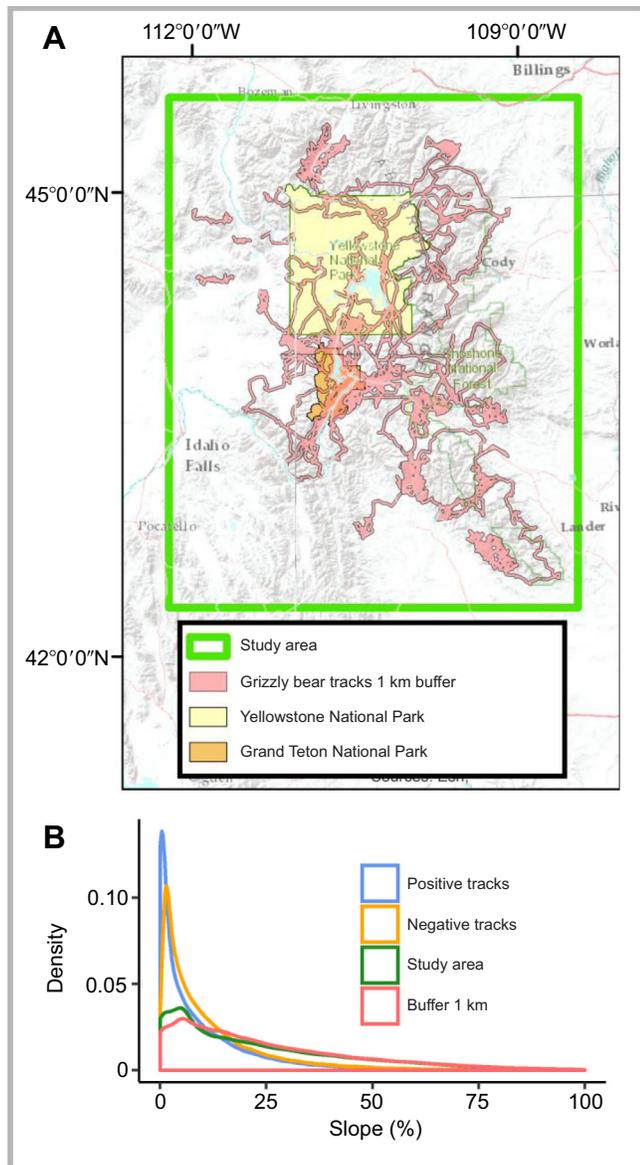


Fig. 5. Map of the Greater Yellowstone Ecosystem. (A) Distribution of grizzly bear paths used in the study. (B) Relative abundance of positive (uphill) and negative (downhill) slopes traveled by grizzly bears in comparison to the percent slope available at random locations within 1 km of each bear's path (buffer) and in the larger study area. The percent slope upon which grizzly bears traveled was determined at each 100 m step and separated into either positive (uphill) or negative (downhill) tracks. Map created using ArcGIS® software by Esri with World Terrain Base map sourced from Esri, US Geological Survey, and National Oceanic and Atmospheric Administration.

gradients at a greater rate than occurred ecosystem wide. For example, while 32% of the 1 km buffer zone around each bear's track had slopes $\leq 10\%$, 68% of the uphill grizzly bear tracks and 61% of the downhill tracks were at slope angles $\leq 10\%$. After correcting all travel speeds to the lowest fix interval of 13 min (Fig. 2), we found that wild grizzly bears moved at an average velocity of $0.61 \pm 0.28 \text{ m s}^{-1}$ (Fig. 6B), well below the most efficient speed of $1.19 \pm 0.11 \text{ m s}^{-1}$ (Fig. 3B). Both males and females traveled slightly faster going downhill than they did uphill, although variance was high.

Males and females chose travel paths that were less than the maximum slope available when moving either upslope or downslope

(Fig. 6A). Bears chose paths across all slopes that averaged 54% less steep than the maximum available, although they chose a slightly less steep path as terrain steepened. By selecting less steep gradients and traveling at the observed velocities, bears reduced their energetic cost by approximately 54% when moving upslope relative to taking the maximum available slope, but they increased their energetic cost when moving downslope by 10% relative to the cost of moving horizontally (Fig. 6C). This increased cost going downhill relative to the horizontal occurred because the energy expenditure measured on the treadmill for downhill locomotion (Fig. 3) was higher than when moving horizontally at the observed speeds of wild bears (Fig. 6B). The highest metabolic rate estimated for wild bears traveling on the steepest terrain ($10.6 \text{ J kg}^{-1} \text{ s}^{-1}$) never exceeded 5 times the resting metabolic rate, even on the steepest slopes. Similarly, the highest metabolic rate when traveling on the steepest terrain (i.e. $12\text{--}13 \text{ J kg}^{-1} \text{ m}^{-1}$; Fig. 6C) never exceeded 3 times the cost of horizontal movement (Fig. 6C).

DISCUSSION

Understanding the energetics of how animals use their environment has broad implications for addressing basic and applied questions in ecology. We hypothesized that plantigrade locomotion by grizzly bears would be more costly than cursorial digitigrade locomotion because of anatomical differences that lead to greater mediolateral forces for bears during movement (Shine et al., 2015). Our findings do not indicate this to be true. Unfortunately, no one has been able to measure the cost of running in bears to determine whether that cost is a linear extension of the cost of walking. Whereas linearity between walking and running is expected based on studies on many other species (Taylor et al., 1970), the cost of a running walk in polar bears is distinctly greater than that predicted from the cost of walking extended to higher speeds (Pagano et al., 2018). However, that gait is used only between 2 and 3 m s^{-1} in grizzly bears (Shine et al., 2015). At faster speeds that would be characteristic of predation events or running from danger, grizzly bears canter or gallop, which are both likely more efficient and therefore less costly than the running walk.

The 46% lower net cost per unit distance for movement by small to large ungulates relative to their plantigrade and digitigrade predators (Fig. 4) suggests a significant advantage favoring the ungulate when fleeing from predators. Even though these differences may in part be due to the longer legs and stride lengths of ungulates relative to their predators, they might also help explain the different hunting strategies of predators when coupled with knowledge of their aerobic capacity. If the maximum metabolic rate measured for the captive bears ($10.6 \text{ J kg}^{-1} \text{ s}^{-1}$, 20% incline) and estimated as the upper sustained limit for GYE grizzly bears ($10.6 \text{ J kg}^{-1} \text{ s}^{-1}$) is representative of their maximum aerobic capacity as suggested by Dunford et al. (2020) for mountain lions, grizzly bears are like mountain lions in having a relatively low aerobic capacity. The aerobic capacity of mountain lions was ~ 5 times the resting metabolic rate, which puts both grizzly bears and mountain lions in the 'non-athletic' grouping of mammals (Weibel et al., 2004). However, when one considers the speed and power of grizzly bear or mountain lion attacks on larger ungulates, classifying them as 'non-athletic' as opposed to 'athletic' seems highly inappropriate and perhaps should be replaced by 'sprinters' and 'endurance runners' to correctly represent both the physiology and ecology of the two different groups of animals.

While one can question whether we measured maximum aerobic capacity, hungry grizzly bears, as ours were in the treadmill studies, are highly food motivated and were unlikely to leave food unless

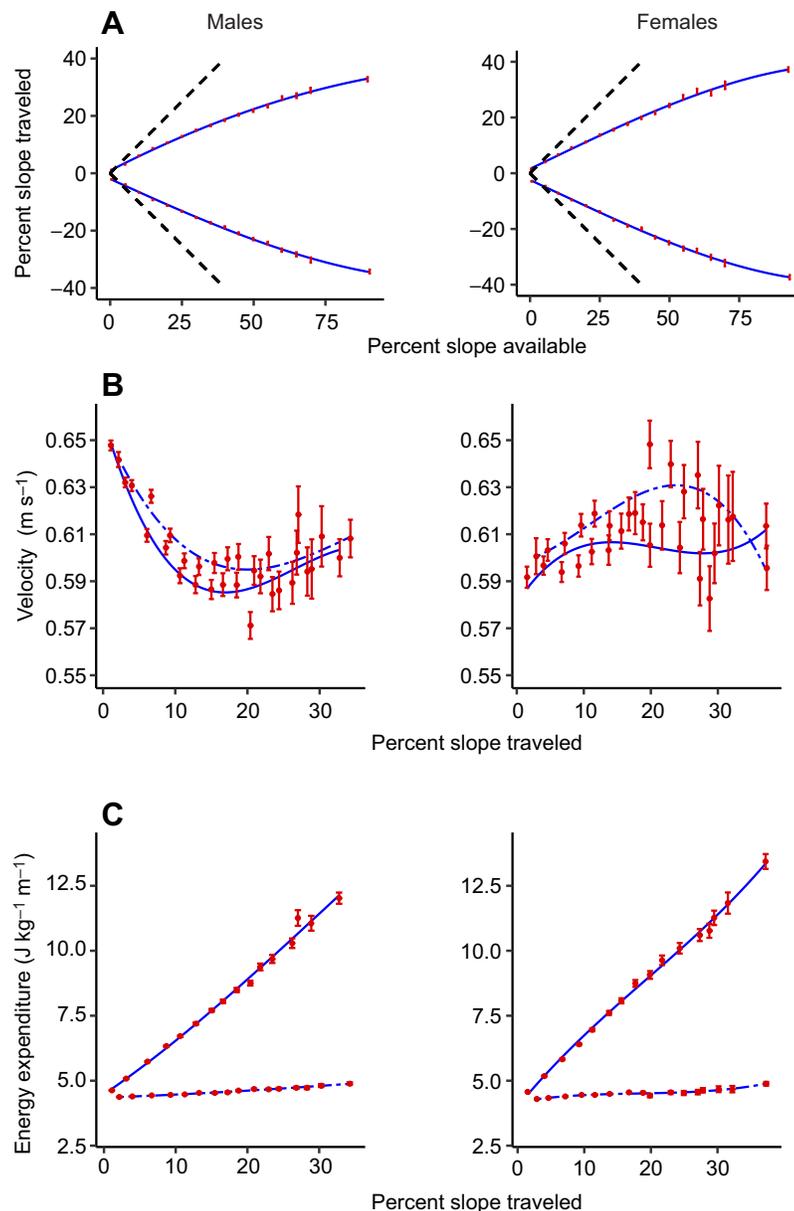


Fig. 6. Relationships of percent slope traveled, velocity and energy expenditure with available slope gradients for grizzly bears in the Greater Yellowstone Ecosystem.

(A) Percent slope traveled versus available. (B) Velocity versus percent slope traveled. (C) Energy expenditure versus percent slope traveled. Steps were grouped every 2.5 percentage points for incline and decline slopes. Red lines indicate standard error of the mean. Dashed black lines in A are the 1:1 relationship between available and traveled slopes. Solid lines in B and C represent uphill travel whereas dashed lines represent downhill travel.

they had reached a physiological limit. Similarly, while Weibel et al. (2004) compared maximum aerobic capacity with basal metabolic rate and we used resting metabolic rate, our bears had fasted for 16 h prior to resting measurements and thus were likely approaching basal conditions. Finally, Weibel et al.'s (2004) athletic animals of a similar size to our grizzly bears had a maximum aerobic capacity that was ≥ 3 times higher than that of non-athletic animals. Thus, small differences in measurement conditions between our study and that of Dunford et al. (2020) on mountain lions in comparison with the studies summarized by Weibel et al. (2004) are unlikely to change the conclusion that grizzly bears and mountain lions have relatively low aerobic capacity.

Grizzly bears use multiple strategies to kill ungulates depending on the vulnerability of the prey (Gunther and Renkin, 1990; Wyman, 2002). The killing of young, vulnerable elk calves (*Cervus canadensis*) that were following their mothers in the open shrub-grasslands of Yellowstone National Park often involved long chases that averaged 8.7 ± 2.0 min and covered 818 ± 149 m, although even

longer chases also occurred (e.g. 58 min, 4812 m). Thus, while relatively long chases were common (84% of all calf hunts), most occurred at an 'easy lope' of 1.4 – 1.6 m s⁻¹ (Cole, 1972; Gunther and Renkin, 1990) before the bear made a short, final sprint. On the relatively flat ground of Pelican Valley where these observations occurred, grizzly bears would have to run at 3.2 m s⁻¹ to reach their aerobic capacity of 10.6 J kg⁻¹ s⁻¹ if the cost of running is a linear extension of the cost of walking (Fig. 3A). However, high-speed predatory chases of either calves or adult elk averaged 8.9 m s⁻¹ and were much shorter in duration (12 ± 5 s) and distance (107 ± 35 m) (Gunther and Renkin, 1990), presumably because the bears were well above their estimated aerobic capacity.

Because the ungulate expends less energy per unit mass than the predator when moving uphill (Fig. 4), one might assume that ungulates living in mountainous terrain should flee from predators by moving uphill. However, the relative increase in the net cost of upslope movement over the cost of moving horizontally is similar for predator (i.e. Fig. 4; 0.63 slope/ 2.92 intercept= 0.21) and prey

(0.40/2.12=0.19). Thus, the predator and ungulate prey should sense the same relative increase in physiological costs of moving upslope over the cost of moving horizontally such that there is no physiological advantage to either. However, the ungulate's lower net cost when moving horizontally when compared with the predator (i.e. the y -intercepts in Fig. 4) and the fact that both the ungulate and the predator will initially use gravity to quickly build up speed going downhill may favor the larger ungulate energetically when fleeing on flat or downhill slopes, but large ungulates are generally not faster than their highly cursorial predators (Garland and Janis, 1993). Thus, aerobic capacity becomes a very important predictor of predatory tactics. For example, grizzly bears typically use either long, low-speed chases that are well below their aerobic capacity when killing vulnerable elk calves or elements of a surprise attack to get close to larger ungulates before sprinting the final distance at speeds that are well above their aerobic capacity. These tactics differ from the extended, high-speed chases that a predator with a higher aerobic capacity, such as wolves, might use (Mattson et al., 1995; Weibel et al., 2004).

Movement paths of wild grizzly bears appear sensitive to the energy costs associated with living in mountainous terrain, as do those of mountain lions (Dunford et al., 2020). For example, both grizzly bears and mountain lions chose lower slope angles and speeds in moving up and down steep terrain, both of which dramatically lowered estimates of energy expenditure per unit time (Figs 5 and 6). The average walking speed of grizzly bears ($0.61 \pm 0.28 \text{ m s}^{-1}$) was 35% less than that of polar bears determined from 10 min fix intervals ($0.94 \pm 0.01 \text{ m s}^{-1}$; Pagano et al., 2018), presumably because the probability of a polar bear encountering a susceptible seal increases with increasing travel speed and distance covered. Even if one extrapolates travel speed to a fix interval of 1 min for grizzly bears (Fig. 2; 0.77 m s^{-1}), their speeds are still well below those of polar bears. However, grizzly bears and humans (0.72 m s^{-1}) have similar walking speeds when traveling on the more modest slope angles chosen by GYE grizzly bears, although grizzly bears maintain higher speeds than humans when traveling on very steep terrain (current study; Irmischer and Clarke, 2018; Lachica and Aguilera, 2005; Minetti, 1995). Similarly, the failure of bears to efficiently recover potential energy when traveling downslope within the speeds and slope angles measured in this study is true for other large mammals, including humans (Halsey and White, 2017).

These basic tenets of how both grizzly bears and people sense and respond to the energy landscape may increase the chance that people will encounter grizzly bears when hiking. For example, National Park Service (1998) construction guidelines for trails recommend that gradients not exceed 10% in steep terrain. With two-thirds of the movement paths of GYE grizzly bears occurring within this gradient range (i.e. 0–10%), it should not be surprising that they choose movement paths similar to humans and commonly use trails built for humans. Indeed, whereas many different factors were involved, 91% of all bear-inflicted injuries in the backcountry of Yellowstone National Park between 1970 and 1994 occurred as people were hiking, either on- or off-trail (Gunther and Hoekstra, 1998). The danger posed by their similarities in travel can be exacerbated by the increasing popularity of trails for other forms of recreation, such as mountain biking when bears and humans encounter each other at high speed with little warning (Servheen et al., 2017). Thus, our findings support management programs, planning processes and outdoor education programs that recognize these inherent similarities in travel between grizzly bears and humans and try to minimize their potential conflict (Coleman et al., 2013a; Gunther and Haroldson, 2020).

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Competing interests

The authors declare no competing or financial interests.

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