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RESEARCH ARTICLE

Energetic costs of locomotion in bears: is plantigrade locomotion energetically economical?

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ABSTRACT

Ursids are the largest mammals to retain a plantigrade posture. This primitive posture has been proposed to result in reduced locomotor speed and economy relative to digitigrade and unguligrade species, particularly at high speeds. Previous energetics research on polar bears (*Ursus maritimus*) found locomotor costs were more than double predictions for similarly sized quadrupedal mammals, which could be a result of their plantigrade posture or due to adaptations to their Arctic marine existence. To evaluate whether polar bears are representative of terrestrial ursids or distinctly uneconomical walkers, this study measured the mass-specific metabolism, overall dynamic body acceleration, and gait kinematics of polar bears and grizzly bears (*Ursus arctos*) trained to rest and walk on a treadmill. At routine walking speeds, we found polar bears and grizzly bears exhibited similar costs of locomotion and gait kinematics, but differing measures of overall dynamic body acceleration. Minimum cost of transport while walking in the two species (2.21 J kg^{-1} m^{-1}) was comparable to predictions for similarly sized quadrupedal mammals, but these costs doubled (4.42 J kg^{-1} m^{-1}) at speeds $\geq$5.4 km h^{-1}. Similar to humans, another large plantigrade mammal, bears appear to exhibit a greater economy while moving at slow speeds.

KEY WORDS: Acceleration, Cost of transport, Metabolism, Overall dynamic body acceleration, *Ursus arctos*, *Ursus maritimus*

INTRODUCTION

A plantigrade posture in which the heel makes contact with the ground during a step is considered to be an ancestral form of locomotion (Lovegrove and Haines, 2004). This posture has been shown to enhance locomotor economy while walking in humans, despite a reduced economy while running relative to digitigrade or unguligrade postures, which enable greater stride length and elastic storage (Carrier, 2016). Members of the family Ursidae represent the largest mammals to have retained a plantigrade posture (Brown and Yalden, 1973), which likely increases their dexterity for digging and climbing and enhances support for their large body mass (McLellan and Reiner, 1994), but may impose a reduced energetic

economy during locomotion (Lovegrove and Haines, 2004; Shine et al., 2015).

Ursids represent a small family of large-bodied terrestrial mammals with a diverse range of diets from specialist carnivores to specialist herbivores and generalist omnivores. Energetics research on ursids has largely focused on their ability to reduce metabolism during hibernation (e.g. Watts et al., 1987; Watts and Cuyler, 1988; Watts and Jonkel, 1988; Tøien et al., 2011). Resting metabolic rates (RMRs) have also been examined in many ursids (Fei et al., 2016; Hurst, 1981; McNab, 1992; Tøien et al., 2011; Watts et al., 1987). Giant pandas (*Ailuropoda melanoleuca*) (Fei et al., 2016) and sloth bears (*Melursus ursinus*) (McNab, 1992) exhibit RMRs that are 18% and 41% less than predictions for similarly sized mammals (Kleiber, 1975), while polar bears (*Ursus maritimus*) (Hurst et al., 1991; Pagano et al., 2018; Watts et al., 1991) and black bears (*Ursus americanus*) (Tøien et al., 2011) exhibit RMRs that are 62% and 23% greater than predictions. This increased maintenance cost in polar bears, and to a lesser extent in black bears, is likely a result of their carnivorous diet, whereas giant pandas are a specialist herbivore and sloth bears an insectivore, both of which impose a lower energetic cost than carnivory (McNab, 1986). Despite this understanding of baseline energetic costs in ursids, the energetic costs of locomotion have received less attention and have only been examined in polar bears. In polar bears, the energetic cost of walking is more than twice that predicted for similarly sized quadrupedal mammals (Hurst et al., 1982a; Øritsland et al., 1976; Watts et al., 1991). Yet, it remains unknown whether this high cost of transport is found across the Ursidae, potentially as a result of plantigrade locomotion, or whether polar bears are distinctly uneconomical walkers as a result of their carnivorous, marine and semi-aquatic lifestyle (Pagano et al., 2018; Williams, 1999; Williams et al., 2002).

Despite the paraphyletic relationship between polar bears and grizzly bears (*Ursus arctos*) (Talbot and Shields, 1996), polar bears exhibit a number of physiological and behavioral adaptations distinct from grizzly bears, likely as a consequence of their marine existence. In addition to being the most carnivorous of the bear species (Stirling and Derocher, 1990), polar bears have larger paws (potentially as an adaptation for swimming; DeMaster and Stirling, 1981), reduced forelimb dexterity (Iwaniuk et al., 2000) and exhibit distinct running kinematics using a transverse gallop compared with the rotary gallop of grizzly bears (Renous et al., 1988). Additionally, a study using tri-axial accelerometers to test the ability of data from grizzly bears to serve as proxies for discriminating basic behaviors in polar bears found that data from grizzly bears failed to reliably discriminate polar bear behaviors (Pagano et al., 2017). This suggests differences in morphology and body movements between the two species while performing similar behaviors (Pagano et al., 2017).

To evaluate whether polar bears have uniquely high energetic costs of locomotion among ursids, we examined the metabolic rates

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of resting and locomotion in polar bears and grizzly bears. To do this, we measured the oxygen consumption, overall dynamic body acceleration (ODBA), stride length and stride frequency of captive polar bears and grizzly bears while at rest in a metabolic chamber and walking on a motorized treadmill. We tested the hypotheses that polar bears differ from grizzly bears in their relationships between speed and oxygen consumption, ODBA, stride length and stride frequency. We compared the costs of locomotion of polar bears and grizzly bears with respect to other plantigrade mammals and digitigrade carnivores, and with estimates based on allometric relationships. We further evaluated the relationship between oxygen consumption and ODBA in polar bears and grizzly bears as a proxy for energy expenditure. In other species, ODBA is strongly correlated with energy expenditure because of the relationship between acceleration and muscle contraction (Gleiss et al., 2011; Wilson et al., 2006), enabling the use of accelerometers to measure energy expenditure in wild animals (e.g. Gómez Laich et al., 2011; Halsey et al., 2009a, 2011; Williams et al., 2014; Wilson et al., 2006, 2012). For example, ODBA has been used to measure instantaneous energetics (e.g. Williams et al., 2014) and to evaluate the energy landscapes of wild animals (e.g. Shepard et al., 2013; Wilson et al., 2012). This is based on the assumption that movement is the primary factor influencing variability in energy expenditure (Costa and Williams, 1999; Gleiss et al., 2011; Wilson et al., 2006). If such relationships are similar in ursids, it could provide a method to remotely measure their energy expenditure. Lastly, we evaluated the locomotor speeds of polar bears walking and running on the sea ice to assess whether preferred locomotor speeds in the wild conform to our energetic predictions.

MATERIALS AND METHODS
Experimental design
We measured oxygen consumption ($\dot{V}_{O_2}$) via open-flow respirometry, and stride frequency, stride length and ODBA via kinematic and accelerometry analyses in polar bears and grizzly bears. Measurements were made within a sealed metabolic chamber (2.7 m×0.9 m×1.2 m) constructed of polycarbonate walls that were reinforced with a steel frame (Technical Services, Washington State University, Pullman, WA, USA) and mounted on the surface of a variable-speed treadmill (T1 Trotter horse treadmill, Horse Gym USA, LLC, Wellington, FL, USA). We further measured the movement rates of wild female polar bears while walking and running on the sea ice of the Beaufort Sea.

Animals
One polar bear (*Ursus maritimus* Phipps 1774) at the San Diego Zoo and seven grizzly bears (*Ursus arctos* Linnaeus 1758) at Washington State University were used for metabolic, acceleration and gait kinematic measurements (Table 1). Additionally, one polar bear at the Oregon Zoo was used for acceleration and gait kinematic measurements (Table 1). The polar bear at the San Diego Zoo was trained over 5 months and conditioned to rest while lying in sternal recumbency and to walk on the moving treadmill while receiving food (i.e. meat and fish) every 20 s. The polar bear at the Oregon Zoo was trained over 8 months to walk on the moving treadmill while receiving food every 20 s. The grizzly bears were similarly trained over 2 months and conditioned to rest while lying in sternal recumbency and walk on the moving treadmill while receiving food every 10–20 s. The research was approved by the Animal Care and Use Committees of the University of California, Santa Cruz, the US Geological Survey, Alaska Science Center, the San Diego Zoo Global, Oregon Zoo and Washington State University (protocols

Table 1. Summary of animals used in this study

Species and individual	Sex	Age	Body mass (kg)	Location
Polar bear 1	Female	31	242	Oregon Zoo
Polar bear 2	Female	16	235	San Diego Zoo
Grizzly bear 1	Male	15	253	Washington State University
Grizzly bear 2	Male	15	239	Washington State University
Grizzly bear 3	Female	14	164	Washington State University
Grizzly bear 4	Female	12	143	Washington State University
Grizzly bear 5	Female	12	142	Washington State University
Grizzly bear 6	Male	2	126	Washington State University
Grizzly bear 7	Female	2	95	Washington State University

04780 and 04952). Polar bear research was further approved under US Fish and Wildlife Service Marine Mammal Permit MA77245B.

To measure locomotor speed in wild bears, we captured one subadult and five adult female polar bears without dependent young on the sea ice of the Beaufort Sea in April 2015 and 2016. Polar bears were located from a helicopter and immobilized with a rapid-injection dart (Palmer Cap-Chur Equipment, Douglasville, GA, USA) containing zolazepam-tiletamine (Telazol®) (Stirling et al., 1989). Procedures were approved by the Animal Care and Use Committees of the University of California, Santa Cruz, and the US Geological Survey, Alaska Science Center. Field research was approved under US Fish and Wildlife Service Marine Mammal Permit MA690038.

Metabolic measurements
$\dot{V}_{O_2}$ measurements were collected over 6–13 min intervals with a minimum of 5 min of steady-state behaviors to ensure equilibration. For both species, at least one resting measurement was taken following an overnight fast to ensure a post-absorptive state. For the grizzly bears, a subsequent resting measurement was taken 3 h after feeding to evaluate the potential effects of specific dynamic action on $\dot{V}_{O_2}$ measurements. Food intake per session ranged from 728 to 963 g (polar bear) and 2000 to 2300 g (grizzly bears).

We used a vacuum pump (FlowKit Mass Flow Generator – 2000, Sable Systems International, Inc., Las Vegas, NV, USA) to draw air in along the lower edge of the treadmill at 700 l min^{-1} during measurements. We monitored flow rates continuously and maintained oxygen levels ≥20% to avoid hypoxic conditions. Sub-samples of air from the exhaust port of the chamber were drawn 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 the percentage of 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 22.2 to 24.6°C (mean 23.9°C) for polar bears and from 18.6 to 34.3°C (mean 28.9°C) for grizzly bears. We converted values to $\dot{V}_{O_2}$ using eqn 4B from Withers (1977), assuming a respiratory quotient of 0.78. All values were corrected to standard temperature and pressure, dry. We calibrated the entire system prior to measurements with dry ambient air (20.95% O_2) and periodically with dry N_2 gas (Fedak et al., 1981). Body mass was measured using a platform scale. We estimated net minimum cost of transport (COT$_{min}$) as the slope and postural cost of activity as the y-intercept of the relationship between $\dot{V}_{O_2}$ (ml O_2 kg^{-1} s^{-1}) and speed (m s^{-1}) (Taylor et al., 1982). We estimated total cost of transport (COT$_{tot}$) by dividing $\dot{V}_{O_2}$ by speed.

Gait kinematics

We measured stride frequency (strides s^{-1}) and stride length (m) at each speed using video from a high-speed camera (Panasonic, Lumix FZ300, 120 frames s^{-1}) and a high-definition video camera (Sony, Tokyo, Japan; HDR-CX260V, 1080 HD, 60p) positioned perpendicular to the treadmill. Video images were analyzed with video-editing and motion analysis software (Corel Video Studio Pro X5, Corel Corp., Ottawa, ON, Canada; ProAnalyst, Xcitex, Woburn, MA, USA). Stride frequency was measured as the average interval for 25 cycles of the front right foot (Heglund and Taylor, 1988).

ODBA

We bolted archival loggers (TDR10-X-340D, Wildlife Computers, Inc., Redmond, WA, USA) to the side of collars such that they were on the left side of the bear's neck (see fig. 1 in Pagano et al., 2017). Archival loggers measured tri-axial acceleration (m s^{-2}) at 16 Hz (range ±20 m s^{-2}) while bears were resting and walking within the metabolic chamber. We also included acceleration and $\dot{V}_{O_2}$ measurements collected from the same polar bear (264 kg) at the San Diego Zoo while she rested during a previous study (Pagano et al., 2018). We estimated the $\dot{V}_{O_2}$ of the polar bear at the Oregon Zoo based on the relationship between speed and $\dot{V}_{O_2}$ derived below. We converted accelerometer measures from m s^{-2} to $\textbf{\textit{g}}$ (1 $\textbf{\textit{g}}$=9.81 m s^{-2}). We used a 2 s running mean of the raw acceleration data to calculate static acceleration (gravitational acceleration) and subtracted the static acceleration from the raw acceleration data to calculate dynamic acceleration (Wilson et al., 2006; Shepard et al., 2008). ODBA was calculated as the absolute sum of dynamic acceleration across the three axes (Wilson et al., 2006).

Preferred locomotor speeds

We measured the movement rates (km h^{-1}) of six female polar bears over 3–13 days while walking or running on the sea ice. Movement rates were derived from global positioning system (GPS) collars (Exeye, LLC, Bristow, VA, USA) with a GPS fix rate every 5 or 10 min. Location data were transmitted via the Iridium satellite system. We used a continuous time correlated random walk (CRAWL) model (https://CRAN.R-project.org/package=crawl; Johnson et al., 2008) in program R (http://www.R-project.org/) to predict locations on a 10 min interval based on GPS locations. The CRAWL model accounts for variable location quality and sampling intervals. We assigned GPS location data an accuracy of 30 m (Frair et al., 2010). We calculated the minimum distance traveled between two successive predicted locations as the great-circle distance (i.e. distance accounting for the Earth's curvature), and calculated movement rate by dividing distance by the duration between predicted locations (i.e. 10 min) in SAS (version 9.3, SAS Institute Inc., Cary, NC, USA). We identified walking and running movements based on archival loggers (TDR10-X-340D, Wildlife Computers, Inc.) attached to the GPS collars, which measured tri-axial acceleration (m s^{-2}) continuously at 16 Hz (range ±20 m s^{-2}). Walking and running were discriminated within the accelerometer data using a Random Forest model (Breiman, 2001) in program R (RandomForest package, https://CRAN.R-project.org/package=randomForest) as described by Pagano et al. (2017). We linked these accelerometer-derived behaviors with their corresponding predicted location data by calculating the percentage time spent walking or running between predicted locations (i.e. 10 min) in SAS. If ≥95% of the time between predicted locations was classified as walking or running, we considered the movement rate during this interval to be indicative of walking or running.

Analyses

We combined our polar bear $\dot{V}_{O_2}$ measurements while walking with $\dot{V}_{O_2}$ measurements similarly recorded using open-flow respirometry from seven sub-adult polar bears (two females and five males) that ranged in body mass from 110 to 235 kg, walking and running–walking on a treadmill (Hurst et al., 1982a,b; Øritsland et al., 1976; Watts et al., 1991). We used least-squares linear regression to evaluate the relationship between $\dot{V}_{O_2}$ and speed. Although Hurst et al. (1982a) proposed a curvilinear relationship between $\dot{V}_{O_2}$ and speed in polar bears as a result of measurements at speeds ≥5.4 km h^{-1}, we evaluated $\dot{V}_{O_2}$ measurements at speeds ≥5.4 km h^{-1} separately as data from wild polar bears indicate they rarely walk this fast (Whiteman et al., 2015) and the predicted gait transition speed for 100–250 kg animals is 5.7–5.3 km h^{-1} (Heglund and Taylor, 1988). We used analysis of covariance (ANCOVA) to evaluate whether the relationships between $\dot{V}_{O_2}$ and speed differed between speeds <5.4 and ≥5.4 km h^{-1}. For grizzly bears, we similarly used least-squares linear regression to evaluate the relationship between $\dot{V}_{O_2}$ and speed. We used ANCOVA to evaluate whether the intercepts and slopes differed between polar bears and grizzly bears in their relationships between $\dot{V}_{O_2}$ and speed. We further used least-squares linear regression to evaluate the relationship between $\dot{V}_{O_2}$ and ODBA and speed and ODBA, and used ANCOVA to evaluate whether the relationship between $\dot{V}_{O_2}$ and ODBA differed between species. ANCOVA was also used to evaluate whether the relationship between stride frequency and speed as well as stride length and speed differed between species. We calculated the mean and distribution of walking and running speeds measured in wild female polar bears on the sea ice. All analyses were conducted in program R and differences of $P \leq 0.05$ were considered significant.

RESULTS

Metabolic rates

RMR of the adult female polar bear averaged 0.27±0.01 ml O_2 g^{-1} h^{-1} (mean±s.e.m., n=5), with a low of 0.25 ml O_2 g^{-1} h^{-1}. In combination with measures previously collected from sub-adult male and female polar bears (Hurst, 1981; Watts et al., 1991), the post-absorptive RMR of polar bears averaged 0.23±0.02 ml O_2 g^{-1} h^{-1} (n=6). Grizzly bears remained active during resting measurements (e.g. head and limb movements) and, thus, their RMRs are akin to zero-velocity measurements (i.e. y-intercept), relating to the postural effect of activity (Schmidt-Nielsen, 1972; Taylor et al., 1970). Zero-velocity metabolic rates of the grizzly bears while post-absorptive averaged 0.55±0.11 ml O_2 g^{-1} h^{-1} (n=5) with a low of 0.30 ml O_2 g^{-1} h^{-1}. Zero-velocity metabolic rates of the grizzly bears 3 h post-prandial averaged 0.50±0.04 ml O_2 g^{-1} h^{-1} (n=5) with a low of 0.36 ml O_2 g^{-1} h^{-1}.

We found a significant difference in the slope ($F_{1,107}$=6.87, P=0.01) and intercept ($F_{1,108}$=58.21, P<0.001) in the relationship between $\dot{V}_{O_2}$ and speed for bears walking at <5.4 km h^{-1} (Fig. 1A) and bears walking at ≥5.4 km h^{-1} (Fig. 2A). Polar bear metabolic rates while walking at <5.4 km h^{-1} exhibited a linear relationship between $\dot{V}_{O_2}$ (ml O_2 g^{-1} h^{-1}) and speed (km h^{-1}): $\dot{V}_{O_2}$=0.44+0.12×speed (r^2=0.42, P<0.001, n=35), and were on average 1.5 times greater than rates predicted for terrestrial carnivores based on body mass and speed (Taylor et al., 1982). At speeds ≥5.4 km h^{-1}, polar bear $\dot{V}_{O_2}$ exhibited a linear relationship with speed: $\dot{V}_{O_2}$=0.41+0.22×speed (r^2=0.32, P<0.001, n=37; Fig. 2A). At speeds ≤4.6 km h^{-1}, grizzly bear $\dot{V}_{O_2}$ similarly exhibited a linear relationship with speed: $\dot{V}_{O_2}$=0.50+0.13×speed (r^2=0.82, P<0.001, n=39), and metabolic rates averaged 1.7 times greater than rates predicted for terrestrial
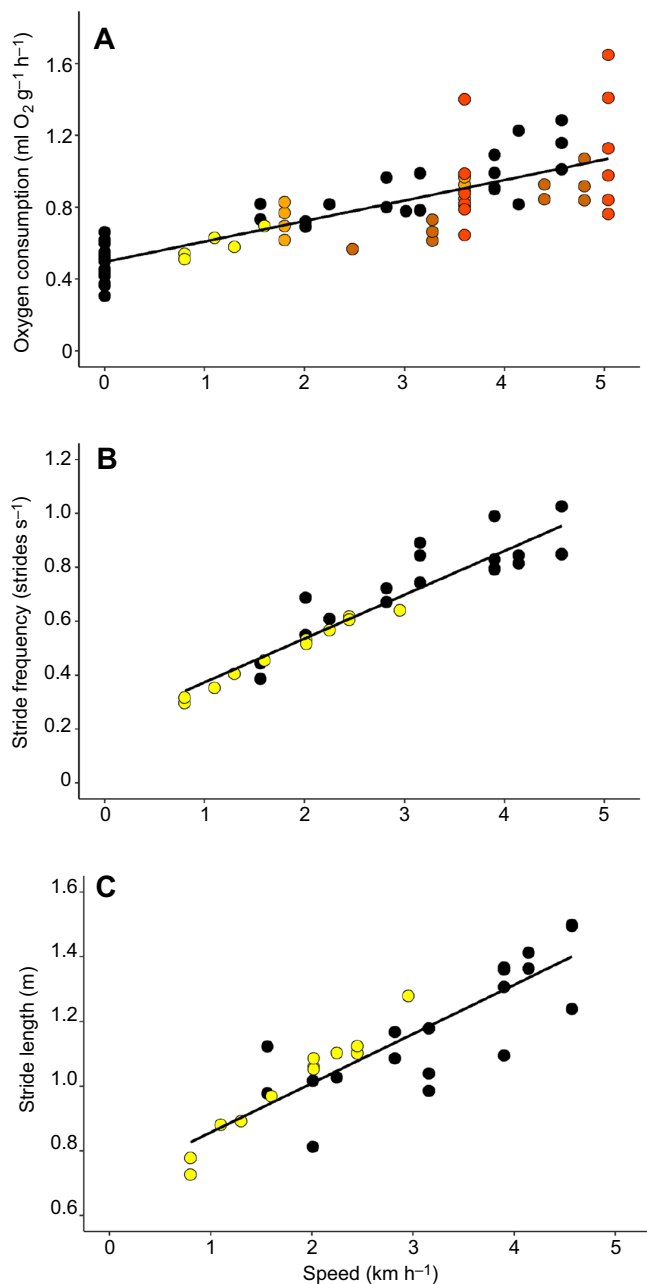
Fig. 1. Relationship between oxygen consumption, gait kinematics and locomotor speed in polar bears and grizzly bears. (A) Least-squares regression (solid line) of mass-specific oxygen consumption in relation to locomotor speed for polar bears and grizzly bears on a treadmill. Points represent individual steady-state measurements for polar bears (yellow circles, present study; orange circles, Hurst et al., 1982a; dark-orange circles, Øritsland et al., 1976; red circles, Watts et al., 1991) and grizzly bears (black circles) (see Results for regression statistics). (B) Least-squares regression (solid line) between stride frequency and speed in polar bears (yellow circles) and grizzly bears (black circles) (see Results for regression statistics). (C) Least-squares regression (solid line) between stride length and speed in polar bears (yellow circles) and grizzly bears (black circles) (see Results for regression statistics).

carnivores based on body mass and speed (Taylor et al., 1982). We found no difference in the slope ($F_{1,70}$=0.06, P=0.80) or intercept ($F_{1,71}$=3.56, P=0.06) in the relationship between $\dot{V}_{O_2}$ and speed for the two species at speeds <5.4 km h^{-1}. Combining data from the two

species, at speeds <5.4 km h^{-1} we found a linear relationship between $\dot{V}_{O_2}$ and speed: $\dot{V}_{O_2}$=0.50+0.11×speed (r^2=0.64, P<0.001, n=74; Fig. 1A). Postural cost of activity (i.e. y-intercept) was 0.50 ml O$_2$ g^{-1} h^{-1} or 2.2 times greater than predictions based on body mass (Taylor et al., 1982). Net COT$_{min}$ was 0.11 ml O$_2$ kg^{-1} m^{-1} (2.21 J kg^{-1} m^{-1}), or 1.1 times greater than predictions based on body mass (Fig. 3) (Taylor et al., 1982). COT$_{tot}$ was lowest at 1.2 m s^{-1} (4.3 km h^{-1}) (Fig. 4). At speeds ≥5.4 km h^{-1}, net COT$_{min}$ was 0.22 ml O$_2$ kg^{-1} m^{-1} (4.42 J kg^{-1} m^{-1}) (Fig. 3).

Gait kinematics

Bears exhibited plantigrade gaits with the toes and metatarsals flat on the ground (Fig. 5; Movies 1, 2). We found no difference in the slope ($F_{1,28}$=0.93, P=0.34) or intercept ($F_{1,29}$=2.43, P=0.13) in the relationship between stride frequency and speed or stride length and speed ($F_{1,28}$=2.26, P=0.14; $F_{1,29}$=2.08, P=0.16, respectively) between the two species. Stride frequency (strides s^{-1}) increased linearly with speed: stride frequency=0.21+0.16×speed (r^2=0.88, P<0.001, n=32; Fig. 1B). Stride length (m) increased linearly with speed: stride length=0.71+0.15×speed (r^2=0.76, P<0.001, n=32; Fig. 1C).

ODBA

The relationship between $\dot{V}_{O_2}$ (ml O$_2$ g^{-1} h^{-1}) and ODBA (g) differed in the slope ($F_{1,29}$=5.49, P=0.03) and intercept ($F_{1,30}$=4.92, P=0.03) between the species. This difference appeared to be predominantly driven by differences in dynamic body acceleration in the sway (z) dimension (Fig. 6). Polar bear $\dot{V}_{O_2}$ increased linearly as a function of ODBA: $\dot{V}_{O_2}$=−0.90+12.33×ODBA (r^2=0.84, P<0.001, n=18; Fig. 7A). Polar bear speed was also strongly predicted by ODBA: speed=−2.92+16.25×ODBA (r^2=0.92, P<0.001, n=18). Grizzly bear $\dot{V}_{O_2}$ increased linearly as a function of ODBA: $\dot{V}_{O_2}$=−0.05+2.03×ODBA (r^2=0.76, P<0.001, n=15; Fig. 7B). Grizzly bear speed was also strongly predicted by ODBA: speed=−4.62+16.12×ODBA (r^2=0.81, P<0.001, n=15).

Preferred locomotor speeds

Walking and running speeds of female polar bears on the sea ice over 10 min intervals averaged 3.4±0.04 km h^{-1} (n=533, Fig. 2B) and ranged from 0.4 to 10.0 km h^{-1}. Only 3% of these movements were at ≥5.4 km h^{-1} (Fig. 2B).

DISCUSSION

Contrary to previous energetic studies on polar bears, our results indicate that polar bears and grizzly bears are energetically similar to other quadrupedal mammals while walking at preferred speeds. In humans, a plantigrade posture while walking has been shown to reduce the cost of transport relative to a digitigrade posture, but incurs a 61% increase in cost of transport while running (Cunningham et al., 2010). Our results similarly indicate that, at routine walking speeds, both polar bears and grizzly bears exhibit costs of transport that are comparable to predictions from other quadrupedal mammals based on their body mass (Taylor et al., 1982), but at speeds ≥5.4 km h^{-1} the cost of transport doubles, greatly exceeding predictions.

Hurst et al. (1982a) proposed a curvilinear relationship between speed and energy expenditure in polar bears as a result of these disproportionately high energetic costs at speeds ≥5.4 km h^{-1}. However, data from wild polar bears indicate they rarely walk this fast (Fig. 2B; Whiteman et al., 2015), which suggests these speeds are likely non-preferred and may require an uneconomical gait. We found COT$_{tot}$ was lowest at 4.3 km h^{-1}, which is almost 1 km h^{-1} greater than the mean walking speed measured in polar bears on the
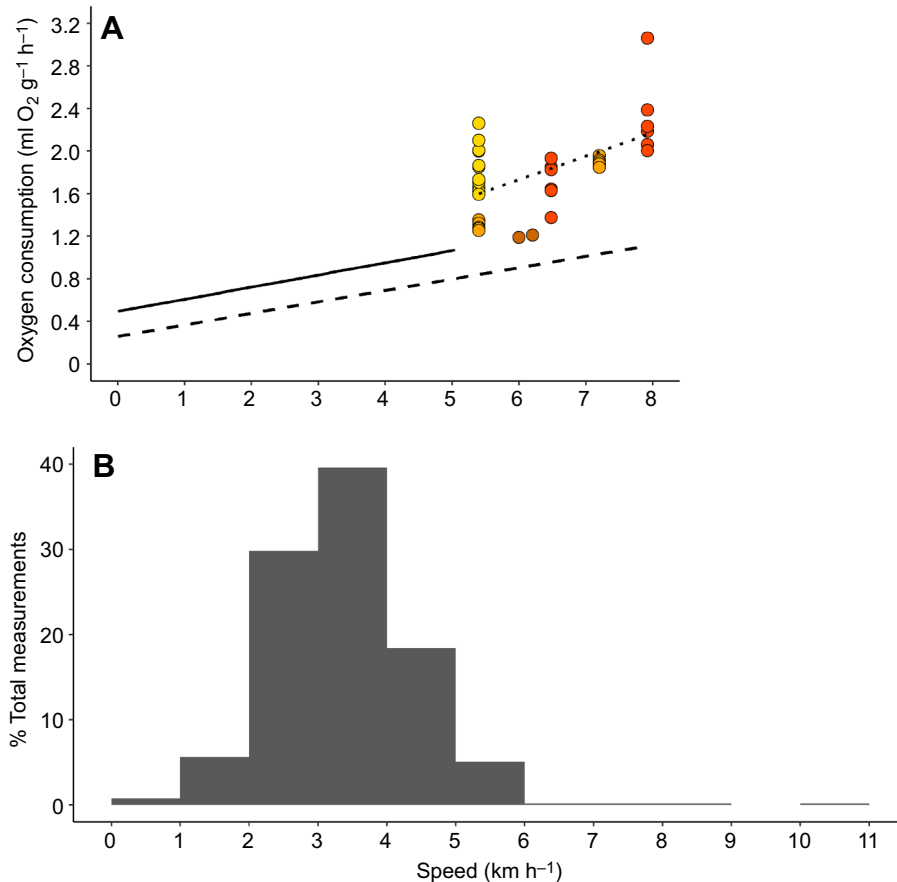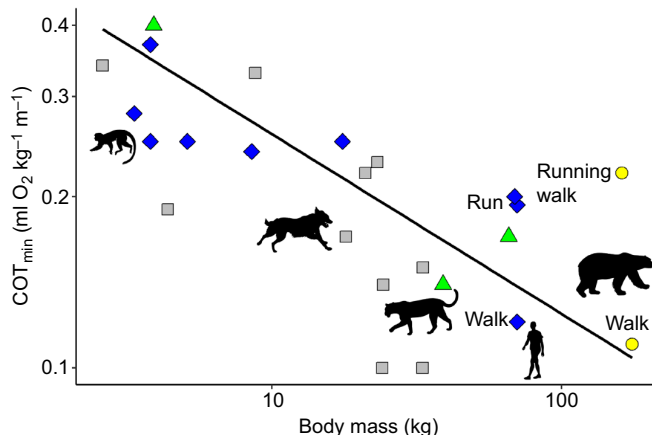
Fig. 2. Relationship between oxygen consumption and locomotor speed for bears moving on a treadmill and locomotor speed of wild polar bears while walking and running on the sea ice. (A) Mass-specific oxygen consumption in relation to locomotor speed. Points represent individual steady-state measurements for polar bears (orange circles, Hurst et al., 1982a; yellow circles, Hurst et al., 1982b; dark-orange circles, Øritsland et al., 1976; red circles, Watts et al., 1991). The solid line is the least-squares regression from polar bears and grizzly bears at <5.4 km h^{-1} (Fig. 1A) and the dotted line is the least-squares regression from polar bears at ≥5.4 km h^{-1} (see Results for regression statistics). The dashed line is the predicted relationship derived from other terrestrial carnivores (Taylor et al., 1982). (B) Frequency distribution of walking and running speeds over 10 min intervals from six female polar bears on the sea ice of the Beaufort Sea in April 2015 and 2016 (*n*=533).
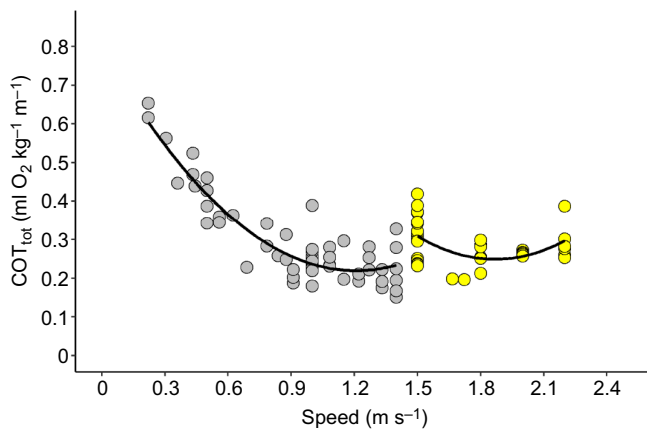
sea ice over 10 min periods. Additionally, field movements would be expected to impose greater energetic costs relative to movements on a treadmill (Bidder et al., 2017). Shine et al. (2015) documented the lack of a trotting gait in grizzly bears and reported transition speeds of ≥7.2 km h^{-1} for running walks and ≥10.8 km h^{-1} for canters. Walking involves storing and recovering energy with each

Fig. 3. Net minimum cost of transport (COT$_{min}$) in digitigrade carnivores and plantigrade mammals. Digitigrade carnivores: canids (gray squares: Bryce and Williams, 2017; Taylor et al., 1982) and felids (green triangles: Taylor et al., 1982; Williams et al., 2014). Plantigrade mammals: primates (blue diamonds: Cunningham et al., 2010; Taylor et al., 1982) and ursids (yellow circles: present study). The solid line is the predicted relationship for COT$_{min}$ of quadrupedal mammals (Taylor et al., 1982). Silhouette images are from http://www.supercoloring.com (https://creativecommons.org/licenses/by/4.0/).

stride via an exchange between gravitational–potential and kinetic energies through an inverted pendulum (Cavagna et al., 1977). However, the benefits of these pendulum mechanics decline at both low and high speeds. At high speeds, animals can trot, run or hop, which allows energy to be conserved through elastic energy recovery (Cavagna et al., 1977). Yet, given their plantigrade posture, bears would be expected to have reduced energy savings from elastic energy recovery relative to unguligrade or digitigrade mammals (Cunningham et al., 2010; Reilly et al., 2007). In humans, plantigrade locomotion enhances pendular mechanics and reduces ground collisional losses in kinetic energy while walking, at the expense of reduced elastic storage at higher speeds (Cunningham et al., 2010). At present, no data exist on the gait mechanics of polar bears at speeds between 5.4 and 7.2 km h^{-1} to better evaluate the causes of these disproportionate energetic costs, and $\dot{V}_{O_2}$ of grizzly bears has not been examined at speeds >4.6 km h^{-1}. Although polar bears seldom walk at these speeds in the wild (Fig. 2B; Whiteman et al., 2015), future research evaluating the gait kinematics and cost of transport of bears at speeds ≥5.4 km h^{-1} would help to better elucidate the aerobic performance of ursids compared with other quadrupedal mammals.

At routine walking speeds, polar bears and grizzly bears exhibited similar energetic costs and gait kinematics. Despite the evolutionary divergence of polar bears from grizzly bears, which has enabled polar bears to exist within the Arctic marine environment and facilitated their ability to swim long distances (Pagano et al., 2012; Pilfold et al., 2017), these adaptations appear to have had little effect on their costs of transport while walking compared with their closest living relative. This result is contrary to most semi-aquatic mammals that have higher costs of transport than

Fig. 4. Mass-specific total cost of transport (COT_{tot}) in relation to locomotor speed in polar bears and grizzly bears. Data are for polar bears and grizzly bears walking at <1.5 m s^{-1} (gray circles) and polar bears walking at ≥1.5 m s^{-1} (yellow circles). The equation describing the second-order polynomial relationship between COT_{tot} and walking speed at <1.5 m s^{-1} is $COT_{tot}=0.40\times speed^2-0.96\times speed+0.80$ ($r^2=0.83$). The equation describing the second-order polynomial relationship between COT_{tot} and speed at ≥1.5 m s^{-1} is $COT_{tot}=0.44\times speed^2-1.64\times speed+1.78$ ($r^2=0.22$).

strict terrestrial or aquatic mammals (Williams, 1999; Williams et al., 2002), and suggests that polar bears are primarily adapted for walking and may incur high energetic costs while swimming (Durner et al., 2011; Griffen, 2018).

Despite walking costs that were similar to those of other quadrupedal mammals, we found both polar bears and grizzly bears have postural costs that are more than double predictions based on other quadrupedal mammals (Taylor et al., 1982). This result is consistent with high resting metabolic rates (Hurst, 1981; Pagano et al., 2018; Watts et al., 1991) and high field metabolic rates in polar bears (Pagano et al., 2018). Taylor et al. (1970) found postural costs ranged from 1.3 to 2.1 times RMR and Cavagna et al. (1977) proposed that this elevated cost may reflect the cost of lifting the center of mass against gravity. However, the postural costs we found are greater than those reported in other large terrestrial mammals. For example, in elephants (*Elephas maximus*), postural costs were 1.4 times greater than predictions (Langman et al., 2012), while in pumas (*Puma concolor*), postural costs were 1.6 times greater than predictions (Williams et al., 2014). Hence, this

increased postural cost in polar bears and grizzly bears may in part be a result of their plantigrade posture as more erect limb postures (e.g. digitigrade and unguligrade) are known to have lower muscle mass and greater effective mechanical advantage (Biewener, 1989; Reilly et al., 2007). We recommend further research to explore the potential causes of these high postural costs in polar bears and grizzly bears. These high costs of activity have important energetic implications for wild polar bears, which appear to be increasing their movement and activity rates in response to climate change (Durner et al., 2017).

Similar to behavior discrimination using tri-axial accelerometers (Pagano et al., 2017), we found the relationship between ODBA and $\dot{V}_{O_2}$ differed between species. This difference appeared to be primarily driven by differences in the sway (*z*) dimension between species (Fig. 6C), which suggests greater side-to-side movement by the grizzly bears while walking. Yet, such movements did not appear to influence either gait kinematics or locomotor costs between species. As our accelerometers were attached to collars on the neck, these movements may reflect differences in head and neck motions between species rather than limb or center of mass movements. Halsey et al. (2009b) found body mass explained most of the variation in the relationship between $\dot{V}_{O_2}$ and ODBA among species. Our adult female grizzly bears wearing accelerometers differed by an average of 89 kg from our adult female polar bears wearing accelerometers, which may have also influenced their side-to-side movements. Our results support Halsey et al.'s (2009b) finding that the relationship between ODBA and $\dot{V}_{O_2}$ is species specific. We recommend further evaluation of the effect of body mass on the relationship between ODBA and $\dot{V}_{O_2}$ in ursids. In particular, ursids are known for extreme seasonal fluctuations in body mass as a result of changes in food availability and winter dormancy (Nelson et al., 1983), and such changes may affect the relationship between ODBA and $\dot{V}_{O_2}$ even on an intraspecific level. Furthermore, the relationships we derived between ODBA and $\dot{V}_{O_2}$ resulted in negative intercepts for both species, which suggests that these relationships need to be further developed in order to use ODBA as a proxy for energy expenditure in these species.

Polar bears and grizzly bears are known to travel extensive distances and have large home ranges relative to other mammals (Ferguson et al., 1999; McLoughlin and Ferguson, 2000; McLoughlin et al., 1999), yet they are primarily ambush and opportunistic predators that typically catch prey through sit-and-wait and stalk behaviors rather than chasing down prey (Garneau et al.,
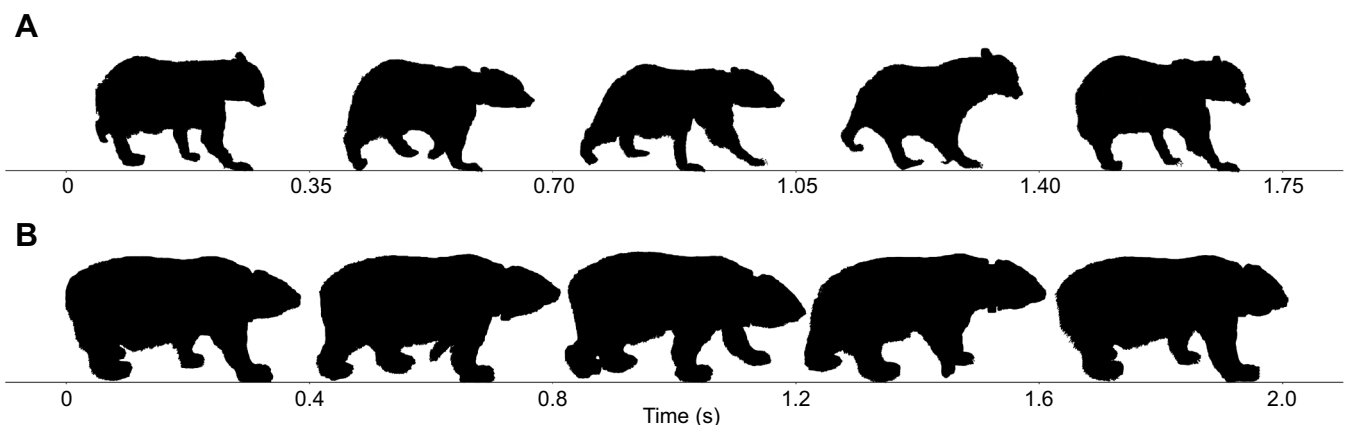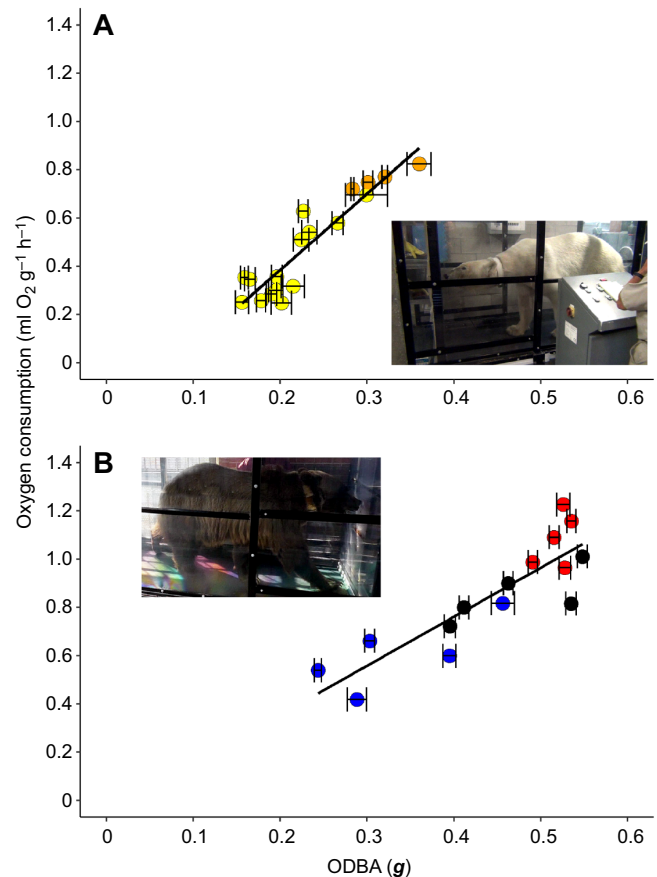

Fig. 5. Plantigrade walking gait of the grizzly bear and polar bear. (A) Single walking stride of an adult female grizzly bear moving on a treadmill at 2.8 km h^{-1} over 1.75 s. (B) Single walking stride of an adult female polar bear moving on a treadmill at 2 km h^{-1} over 2 s.
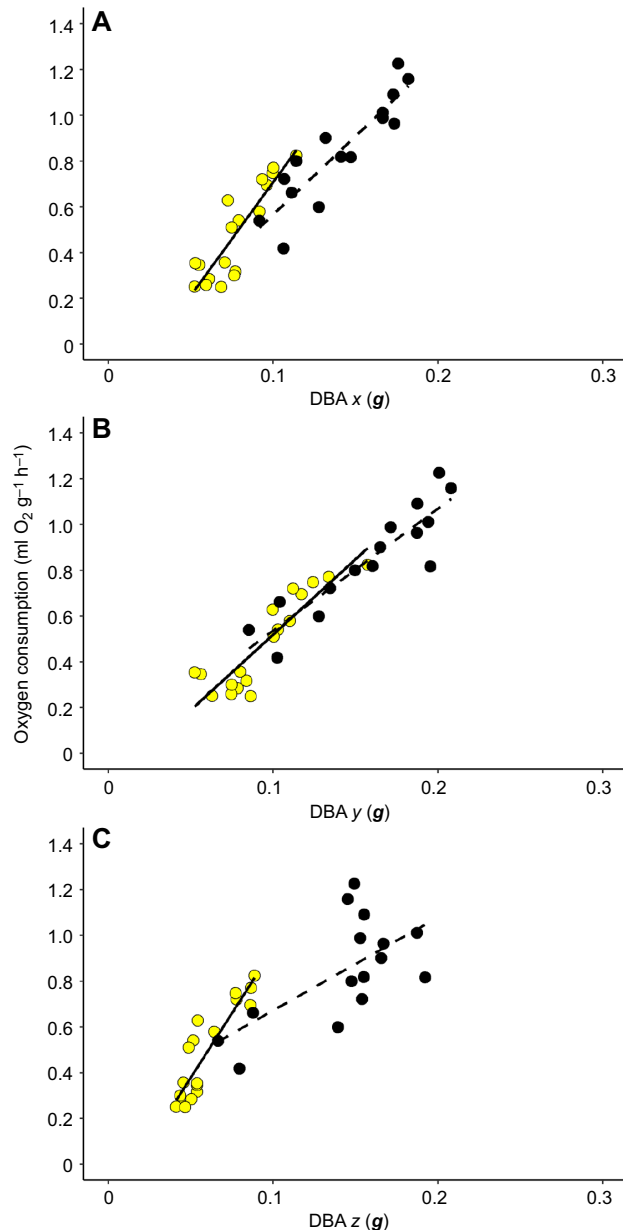
Fig. 6. Relationship between oxygen consumption and dynamic body acceleration (DBA) in polar bears and grizzly bears. (A–C) Least-squares regression of mass-specific oxygen consumption and mean absolute DBA in the surge (x; A), heave (y; B) and sway (z; C) dimension from two adult female polar bears (yellow circles, solid line) and three adult female grizzly bears (black circles, dashed line) resting and walking on a treadmill. Points are mean steady-state measurements.

Fig. 7. Relationship between oxygen consumption and overall dynamic body acceleration (ODBA) in polar bears and grizzly bears. (A) Least-squares regression of mass-specific oxygen consumption and mean ODBA from two adult female polar bears (polar bears 1 and 2; yellow and orange circles, respectively) resting and walking on a treadmill. Points are mean (±s.e.m.) steady-state measurements (see Results for regression statistics). (B) Least-squares regression of mass-specific oxygen consumption and mean ODBA from three adult female grizzly bears (grizzly bears 3–5; red, blue and black circles, respectively) resting and walking on a treadmill. Points are mean (±s.e.m.) steady-state measurements (see Results for regression statistics).

2007; Pagano et al., 2018; Stirling, 1974; Stirling and Derocher, 1990). Our results provide the physiological basis for these seemingly contradictory behaviors. Both species exhibit economical costs of walking, facilitated by their plantigrade posture. However, like humans, this comes at the expense of a less economical cost while moving at higher speeds. Observations of polar bears chasing down flightless geese (Iles et al., 2013) have inspired analyses that found this hunting strategy to be energetically profitable (Gormezano et al., 2016). Nevertheless, our results highlight the elevated energetic demands for polar bears to chase down their prey compared with traditional sit-and-wait tactics. This reinforces the importance of Arctic sea ice to enable polar bears to efficiently capture prey.

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Movie 1. High-speed video (120 frames s^{-1}) showing the plantigrade walking gait of an adult female polar bear walking on a treadmill at 2 km h^{-1}.
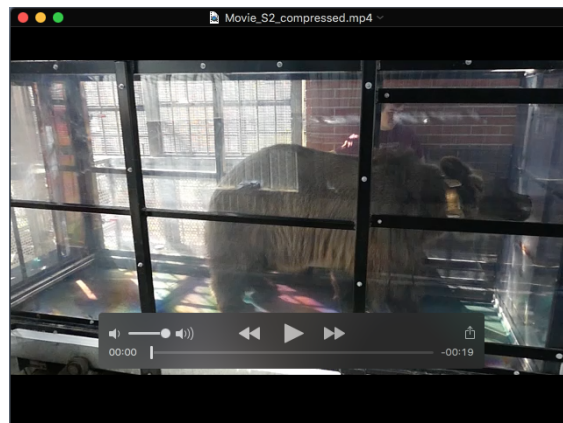
Movie 2. High-speed video (120 frames s^{-1}) showing the plantigrade walking gait of an adult female grizzly bear walking on a treadmill at 2.8 km h^{-1}.