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Energy landscapes of Kodiak brown bears: a comparison of accelerometer and global positioning system-derived estimates

S. P. Finnegan^{1,6,7*}, A. M. Pagano^{2,5}, N. J. Svoboda³, S. L. Schooler¹ and J. L. Belant⁴

Abstract

Within optimal foraging theory animals should maximize their net energy gain while minimizing energetic costs. Energetic expenditure in wild animals is therefore key to measure proxies of fitness. Accelerometers are an effective tool to study animal movement-based energetics, but retrieval of the device is usually required and often difficult. Accelerometers measure movement across three axes (x , y , and z) and can be calibrated to measures of oxygen consumption from captive animals, providing estimates of overall energy expenditure. Measuring energetic expenditures using a global positioning system (GPS) approach could provide an alternative method to study energetic ecology. This technique uses locomotor speeds across a range of slopes from successive GPS locations, which can be linked to the energy expenditure from captive individuals. We compared accelerometer and GPS methods of energetic expenditures in free-roaming brown bears (*Ursus arctos*) on the Kodiak Archipelago, Alaska, USA. We then applied the GPS method to examine how multiple factors influenced brown bear movement-based daily energetic expenditures (MDEE). We found that while the two energetic measurements differed (Wilcoxon signed rank test: $V = 2116$, $p < 0.001$), they were positively correlated ($r = 0.82$, $p < 0.001$). The GPS method on average provided 1.6 times greater energy estimates than the accelerometer method. Brown bears had lower MDEE during periods of high food abundance, supporting optimal foraging theory. Reproductive status and age did not influence MDEE, however movement rates had a positive linear relationship. Energetic ecology is important for understanding drivers of animal movements. Data from GPS collars can provide useful information on energetic expenditures, but should be validated for the specific taxa, ecosystem, and GPS sampling rate used. Additionally, while movement-based estimates of energy expenditure can elucidate the mechanisms driving habitat use decisions, they may not fully reflect an animal's overall energy demands. Brown bear movement-based energetic expenditure was influenced by food abundance and movement rates, which highlighted the importance of access to prime foraging sites to enhance energetic efficiency.

Keywords Accelerometers, Large carnivore, Daily energetic expenditure, Ecological energetics, GPS, Optimal foraging theory, *Ursus arctos*

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Background

Optimal foraging theory suggests animals will minimize energetic costs while maximizing their net energy gain [49]. Energy is attained through consumption of resources and used to meet metabolic demands, growth, reproduction and activity, it is therefore a key currency by which we can examine a proxy of animal fitness at individual and population levels [7]. Although internal metabolism and heat production account for the largest portions of energy expenditure, physical activity can result in the greatest energetic fluctuations [68]. The variation in environmental factors which continually impact an animal's cost of transport, such as vegetation type, slope and speed, have been termed the 'energy landscape' [69]. Quantifying an animal's energetic landscape allows us to identify the biological and physical constraints underpinning their movement ecology [12].

Among large carnivores, which are often required to travel large distances to obtain food and mates, energetic demands related to movement can account for extensive portions of daily energy allocation ([35, 56, 64]. In addition, energetic demand increases with body size [4] and there is a selective advantage to minimize locomotor costs [8]. Carnivore movement decisions are affected by many landscape factors, and they will often minimize travel costs where possible [8]. For example, many species of large felids travel along human roads and trails [16], while wolves (*Canis lupus*) often travel along anthropogenic and natural linear features to reduce energetic costs [8]. An efficient movement strategy must be assessed in relation to the environment the animal is traversing, as movement costs can vary greatly depending on temporal and spatial factors [53]. In landscapes where resources are spatially heterogeneous, animals are predicted to forage in areas that offer the greatest cost minimization and net energetic uptake [40]. The role of energy landscapes in driving animal movement decisions remains poorly studied across many taxa [53].

Studying the energetic expenditures of free-ranging wildlife is challenging [30]. Energetic variation has been estimated using fluctuations in measurements of attached heart monitors [29] or doubly labeled water [48, 65]. Recent advances in technology, specifically tri-axial accelerometers, are now used to study energetic ecology [45, 46]. Accelerometers measure movement across three axes (x , y , z) and can be calibrated to measures of oxygen consumption from captive animals, providing estimates of overall energy expenditure [70], what we refer to as the "accelerometer method". The conversion of accelerometer data to a unit of energetic measurement is known as dynamic body acceleration (DBA) and represents fluctuations in velocity due to animal movements [28, 70].

Advantages of accelerometers include their relatively low cost and long battery life [5]. However, obtaining the stored data typically requires collection of the device upon completion of the study [6], which can be challenging due to the remote locations and wide-ranging behavior of some species, such as large carnivores. A supplementary approach to estimate energetic expenditure from wild animals fitted with global positioning system (GPS) radio collars involves the use of locomotor speeds across a range of slopes from successive GPS locations, which can be linked to the energy expenditure from captive individuals moving at varying speeds and slopes [12, 17], what we refer to as the "GPS method". While this technique does not gather energetic data at the same resolution as an accelerometer, it has an advantage over accelerometers since the data can be downloaded remotely from the animal and thus, does not require retrieval of the device [61]. This GPS method potentially provides researchers, already studying movement ecology using GPS collars, the additional capability of investigating the energetic ecology of their study species. Specifically, GPS-derived estimates of energy expenditure should be effective at measuring movement-based energetic costs that result from point-to-point-based movements, while accelerometer-derived estimates should reflect all movement-based energetic costs regardless of whether the animal changed its spatial location. It is important to note however, that neither method can account for non-movement based energy expenditure, such as lactation, growth, thermoregulation and digestion.

Brown bears (*Ursus arctos*) are a generalist species which occupy a wide variety of habitats [2]. They display extensive variation in diet across seasons, which influences home range sizes and energetic expenditures [43]. For instance, brown bears on the Kodiak Archipelago, Alaska, USA, occupy larger home range sizes during summer when salmon and berries are highly abundant [1, 19]. However, in late fall when food is less available, bears may increase movements in search of food [19] or reduce movement before denning [20]. Brown bears exhibit sexual size dimorphism, where larger-bodied males often occupy larger home ranges than smaller females [15, 19]. Although likely due to greater energetic demands associated with larger body sizes, these space use differences may also be a result of mate-seeking behavior, whereby males use larger ranges to increase reproductive success [14].

Infanticide is the killing of conspecific offspring for reasons including enhanced reproductive opportunities, competition and cannibalism, and is commonly reported in brown bears [59]. Female bears with dependent young may restrict their space use to reduce the risk of

infanticide [14], or alternatively they may increase movements to obtain more resources to support increased energetic demands associated with cub-rearing [42]. Age can also play an important role in home range dynamics due to age-related dominance [15]. Age is closely related to body size, with older individuals often reaching greater body sizes until reaching an asymptote and can display greater dominance and hold larger home ranges [15]. As brown bears must gain enough fat reserves to survive denning, understanding their energetic ecology and the potential biological and behavioral factors which may influence it, are important considerations for conservation and management.

We first aimed to compare the use of GPS-derived estimates of energy expenditure relative to more intensively collected accelerometer-derived (ACC) estimates in wild, free-ranging brown bears on the Kodiak Archipelago, Alaska, USA. Previous research has applied the use of GPS energy estimates to wild brown bears in the Yellowstone ecosystem [12], however no prior work to our knowledge has simultaneously compared this method to accelerometer-derived estimates in brown bears. We then applied the GPS method as a case study on a larger sample size of brown bears to determine movement-based daily energetic expenditures (MDEE) in relation to intrinsic (reproductive status, age, movement rate), spatial (terrain roughness, distance to salmon [*Oncorhynchus* spp.] streams) and temporal (food abundance period, ambient temperature) factors. We predicted that bears would have increased energetic expenditures in the high food abundance period due to increased movements to monopolize food resources during this time [19]. Alternatively, due to the effects of mate-seeking behavior on bear movement in spring, bears may exhibit higher energetic costs during these low food abundance periods. We further predicted that reproductive status would affect movement-based energetics, where females with dependent young would constrict space use to reduce risk of infanticide and thus have lower movement-based energetic expenditures compared to males and solitary females. Lastly, we predicted older individuals with larger body sizes would move greater distances as they can dominate resource rich areas over younger individuals, and thus incur greater energetic costs.

Methods

Study area

Afognak (58.3279° N, 152.6415° W) (1809 km²) and Raspberry (58.0708° N, 153.1876° W) (197 km²) islands are in the Kodiak Archipelago, Alaska, USA, 5 km north of Kodiak Island and separated by a 1.5-km-wide strait (Fig. 1). Both islands contain rolling mountains, with elevations to 739 m on Afognak Island and 732 m on

Raspberry Island. The archipelago has a subarctic maritime climate, with a mean annual temperature of 2.1 °C (− 0.9° to 12.9 °C monthly mean range) and total mean annual precipitation and snowfall of 198 and 175 cm, respectively [50]. Sitka spruce (*Picea sitchensis*) is the dominant tree species on Afognak, while devil's club (*Oplopanax horridus*), blueberry (*Vaccinium ovalifolium*), salmonberry (*Rubus spectabilis*), and willow (*Salix* spp.) are dominant understory species [62]. Chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon migrate and spawn throughout the island's streams and lakes (Alaska Department of Fish and Game, unpublished data). Because of close proximity and presumed inter-island movements of brown bears, we considered Afognak and Raspberry islands a single study site, hereafter referred to as Afognak Island. Sitkalidak Island (57.1030° N, 153.2356° W, Fig. 1) (300 km²) is separated from Kodiak Island by a 320- to 3200-m-wide strait and is located about 91 km south of Afognak Island. Sitkalidak Island has steep mountains with elevations to 672 m. Several streams provide spawning habitat for four species of Pacific salmon. On Afognak and Sitkalidak islands, brown bears rely seasonally on salmon, vegetation and berries, and to a lesser degree, ungulate prey and other marine-derived food [1, 62].

Animal handling

We captured bears during 2019–2020 using standard aerial darting techniques with an R44 helicopter and rifle-fired (CapChur SS cartridge-fired rifle) darts containing Telazol (Zoetis Services LLC; Parsippany, USA) [57]. We fitted animals with global positioning system (GPS) collars (model Vertex Plus-4, Vectronic, Berlin, Germany), with built in tri-axial accelerometers sampling continuously at 32 Hz (± 8 g range). We programmed collars to attempt a relocation every 60 min then release from the animal 21–24 months post-capture. We also inserted a leather link designed to degrade after 2 years as a secondary drop-off mechanism [22]. We extracted a vestigial upper premolar from bears to estimate age using cementum annuli counts [11]. Body weight data were unavailable for this study, however as age is closely associated with body size, with older individuals commonly larger until reaching an asymptote [58], we used age as a proxy for body weight. We assigned each bear to an age category (young adult, adult and mature adult) to examine how age and associated body mass may influence energetics. Young adults were 3–6 years old and unlikely to reproduce (although age of first reproduction in brown bears varies) [41]. Adult bears were 7–12 years old and considered breeding adults, while mature adults were >12 years old and likely to have reached full skull size [32]. We recorded sex and for females, evidence

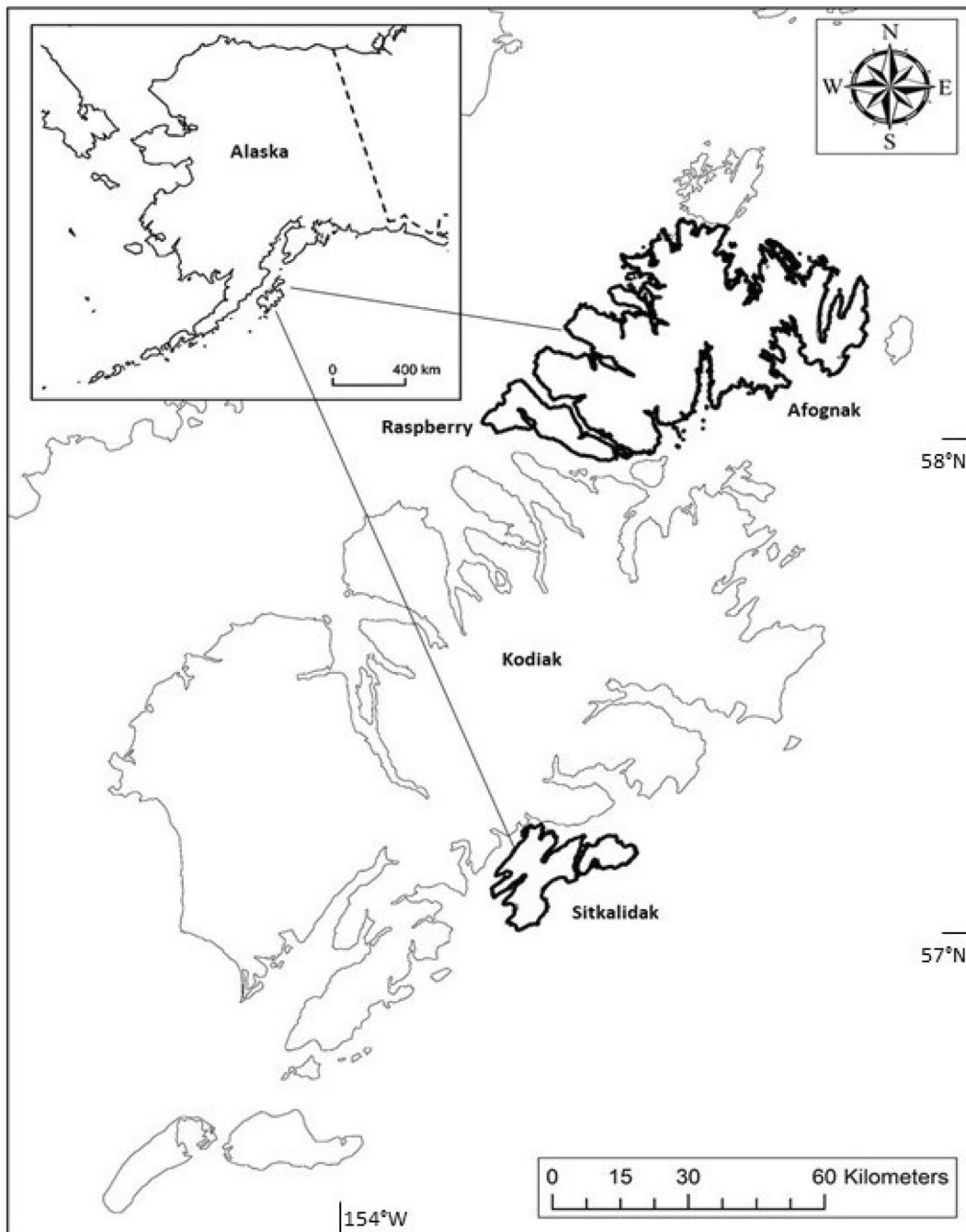


Fig. 1 Location of Afognak, Raspberry and Sitkalidak islands, Kodiak Archipelago, Alaska, USA

of lactation and presence of young. No females with dependent young of the year (<1 years old) were captured, therefore dependent young in this study refers to cubs 1–3 years old. We positioned bears sternal following handling to recover at their capture sites. All animal handling procedures were approved by the State University of New York College of Environmental Science and

Forestry Institutional Animal Care and Use (IACUC) (protocol 180503) and Alaska Department of Fish and Game (ADFG; IACUC protocol 0030-2017-37).

ACC and GPS energy calculation

To derive energetic expenditure from accelerometer data, we calculated overall dynamic body acceleration (ODBA)

from eight brown bears and converted values to rates of oxygen consumption (Vo_2) based on relationships derived from captive brown bears walking on a motorized treadmill, where Vo_2 (ml/kg/min) = $0.069 + 31.972 \times \text{ODBA}$ [47]. We converted Vo_2 to joules by multiplying by 20.08. We excluded data from all individuals for 5 days post-capture to account for potential recovery effects on movement behavior [60]. We used a 2-s running mean of the raw acceleration data to determine static acceleration and then subtracted from the raw data to estimate dynamic acceleration [47, 54, 70]. The ODBA value was calculated as the absolute sum of dynamic acceleration across all three axes (surge, heave, and sway) (Additional files 2, 3):

$$\text{ODBA} = |A_x| + |A_y| + |A_z|,$$

where A_x , A_y , and A_z are the derived dynamic accelerations at any point in time corresponding to the three orthogonal axes of the accelerometer.

Using data collected from GPS collars, we calculated movement rates (km h^{-1}) between successive hourly locations. To reduce uncertainty, we only considered successive locations <63 min apart and removed fixes with poor dilution of precision rates. We determined the minimum distance between each location as the great-circle distance (accounting for the curvature of the Earth's surface), and derived a movement rate by dividing the distance by the duration between locations [47]. We measured the slope between locations using the R package *elevatr* [34].

We derived the ACC measure of energetic expenditure using ODBA combined with the equations for moving up or downhill based on associated GPS locations. The GPS method used the relationships between slope and speed (m s^{-1}) with energy expenditure derived from nine captive brown bears [12] to measure energy expenditure based on the hourly movement rate and slope derived from successive GPS locations. At horizontal slopes (i.e., 0°), energy expenditure $\text{J kg}^{-1} \text{ s}^{-1} = 2.81 + 2.45 \times \text{speed}$; at inclines $>0^\circ$ and $<15^\circ$, energy expenditure = $2.93 + 6.05 \times \text{speed}$; at inclines $\geq 15^\circ$, energy expenditure = $2.76 + 10.63 \times \text{speed}$; and at declines (i.e., $<0^\circ$), energy expenditure = $2.71 + 4.74 \times \text{speed} - 2.48 \times \text{speed}^2$ [12].

Application to wild bears

Using GPS collars retrieved from wild brown bears we determined and compared the ACC- and GPS-derived energetic expenditure. We then applied the GPS method to a dataset from 28 brown bears on Afognak and Sitkalidak islands. We determined movement-based daily energetic expenditure (MDEE) by averaging hourly

energetic measurements for each individual brown bear ($\text{J kg}^{-1} \text{ h}^{-1}$).

Environmental variables

We created a terrain roughness index (TRI) from a 30-m-resolution digital elevation model for the Kodiak Archipelago (Kodiak Island Borough GIS and Map Center, unpublished data) using ArcGIS (10.7.1, ESRI 2018, Redlands, CA). This index calculates the difference in elevation from a center cell value to the eight surrounding cells by squaring each of the eight elevation difference values to make them all positive, summing them, and taking the square root [52]. This index characterizes irregularity in elevation within a given unit [55], and can be an important factor that impedes or facilitates animal movement and subsequent energetic expenditures. We assigned a TRI value for each brown bear location and then determined the circular average daily TRI value to assess its effect on energetic expenditure. Due to the importance of salmon to bears and potential energetic implications of foraging, we calculated the distance from each GPS location to the nearest anadromous salmon stream (Alaska Department of Fish and Game, unpublished data), and determined the average daily distance for each animal. We divided GPS data into two periods to assess how fluctuations in food availability influenced MDEE. The high food abundance period was 1 July–31 September, corresponding with spawning salmon and ripe berries, important foods for brown bears [1, 3, 62]. The low food abundance period was 1 April–30 June and 1 October–31 November, reflecting when dominant foods were less available. We excluded data collected during December–March as many animals enter denning during this period. Ambient temperature readings were recorded at each GPS location via the GPS collar and we calculated daily means to test its influence on MDEE. Temperature readings collected from GPS collars are strongly correlated with temperature readings from nearby weather stations and considered suitable for these purposes [18].

Energy landscape

To create visual examples of energetic expenditures we used the inverse distance weighted interpolation tool in ArcGIS [13] to construct energy landscapes for an individual male and female brown bear on Afognak Island. We created maps for both animals that displayed energetic measurements across the landscape from the ACC and GPS methods (4 maps total). We used the inverse distance weighted interpolation tool as we had a large sample of location data that represented the range of observed values for that energy surface [39].

Statistical analyses

We conducted all analyses using R statistical software [51]. We tested our data for normality and found the ACC and GPS measures of energetic expenditure were not normally distributed. We used a Wilcoxon signed rank test [24] to test whether GPS and ACC measurements differed. We used the non-parametric Spearman’s rank correlation test to measure the strength and direction of the association between the two energy measurements [23]. We constructed 11 a priori models and a null model to assess the influence of internal (reproductive status [M= male, F= female, FY= female with dependent young], age and movement rate [km h⁻¹]), spatial (TRI, distance from nearest salmon spawning streams), and temporal (food abundance period, temperature) factors on brown bear MDEE derived from the GPS method (Additional file 1: Table S1). We used a Pearson’s product-moment correlation coefficient (*r*) to diagnose multicollinearity among dependent variables, and assumed it did not influence model results if $|r| < 0.70$.

We used generalized additive mixed models (GAMMs) to examine factors influencing MDEE using the ‘mgcv’ package in R [72]. This model type allowed flexibility to handle nonlinear predictor variables. We applied a cubic spline smoothing factor to nonlinear variables and set individual bear ID as a random factor [71]. We selected

our top model based on the lowest Akaike Information Criterion, adjusted for small sample sizes (AICc), and only models with $\Delta_i \leq 2$ were selected for further consideration [10]. Unlike generalized linear models, the likelihood ratio statistic of a GAM does not follow a Chi-square distribution and consequently, *p*-values are only approximate [71, 74]. However, if observed *p*-values are approximately in the upper 2.5%, results can be interpreted with more confidence [74]. Consequently, we considered only model variables with *p* values < 0.025 as strongly significant, and variables with *p* values 0.05–0.025 as marginally significant.

Results

We estimated hourly energetic data using the GPS and ACC method for eight brown bears (M=3, F=3, FY=2) from Afognak and Sitkalidak islands during September 2019–November 2020 (*n* = 23,024, Additional file 1: Table S2). The energetic expenditure was greater using the GPS method (median = 10,198 J kg⁻¹ h⁻¹) compared to the ACC method (median = 5351 J kg⁻¹ h⁻¹) (*V* = 2116, *p* < 0.001), with paired daily measurements positively correlated (*r* = 0.82, *p* < 0.001; Fig. 2). Visual inspection of the inverse distance weighted energy landscapes

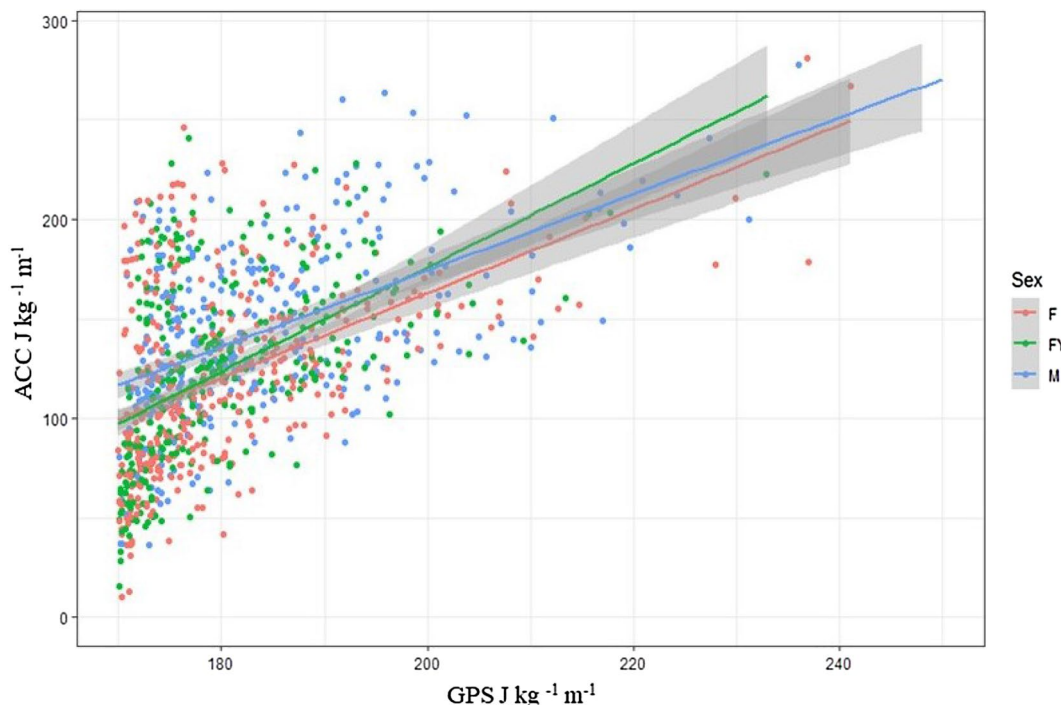


Fig. 2 Correlation between daily average GPS- (GPS method) and accelerometer- (ACC method) derived measures of energetic expenditure (J kg⁻¹ m⁻¹; *r* = 0.82, *p* < 0.001) for eight brown bears (F = female, FY = female with young, M = male), Afognak and Sitkalidak islands, Alaska, USA, September 2019–November 2020

for a male and female bear suggested more energetic variation with the ACC method (Fig. 3).

We applied the GPS method of energetic expenditure to data collected from 28 brown bears (M=6, F=9 and FY=13) during September 2019–November 2020 for a total of 3509 bear days (M=769, F=1079, FY=1661). The median MDEE was 10,303 (standard deviation=33,432) J kg⁻¹ h⁻¹ for males, 10,301 (standard deviation=19,201) J kg⁻¹ h⁻¹ for solitary females and 10,307 (standard deviation=6470) J kg⁻¹ h⁻¹ for females with young. Our full model was most supported (AIC=−21,726, model weight=1, R²=0.96) with no competing models. We found internal (movement rate) and temporal (high food abundance period) factors had the greatest effects on brown bear movement-based energetic expenditure (Table 1). Brown bears had lower energetic expenditures in the high food abundance period (*p*=0.001), and movement rate was positively related to MDEE (R²=0.96, *p*=0.001; Fig. 4). Decreasing ambient temperatures were associated with greater movement-based energetic costs (*p*=0.010). Increasing terrain roughness was associated with marginally significant increases in energetic expenditures (*p*=0.037, edf=1.000), while closer proximity to salmon streams (*p*=0.031, edf=1.000) was also associated with marginally significant increases in expenditure.

Table 1 Parameter estimates for generalized additive mixed models (GAMM) on daily movement-based energetic expenditure of 28 brown bears, Afognak and Sitkalidak islands, Alaska, USA, September 2019–November 2020

Covariate	edf	Parameter estimate	t/f score	p-value
Intercept		5.124	4326.987	0.001
Sex—female with young		−4.830	−0.647	0.517
Sex—male		7.526	0.087	0.930
Age—mature		2.569	0.035	0.972
Age—young		5.060	0.563	0.573
Food period—high		−2.443	−5.333	0.001
Temperature		−1.026	−2.559	0.010
Movement rate		3.911	276.628	0.001
Terrain roughness	1.000		4.317	0.037
Distance to salmon streams	1.000		4.621	0.031

Effective degrees of freedom = edf, values in bold are significant (*p* < 0.05)

Discussion

High-frequency accelerometer data can measure instantaneous energetic costs as animals move across changing landscapes in search of resources [17, 46, 66]. Although the benefits of this technology are immense, challenges remain, in particular the collection of the device upon study completion [6]. Accelerometers are also data intensive due to their continuous high-frequency

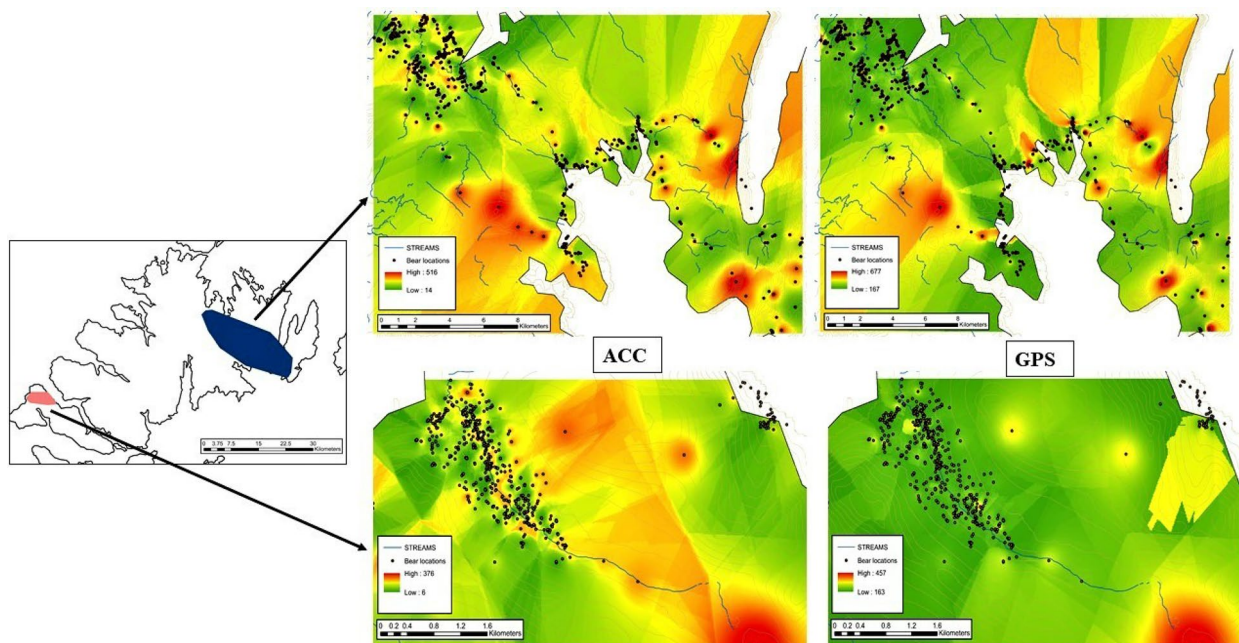


Fig. 3 Estimated energy landscapes for a male (top) and female (bottom) brown bear using accelerometer- and GPS-derived measures of energetic expenditure (J kg⁻¹ m⁻¹), Afognak Island, Alaska, USA, 1 July–4 August 2020

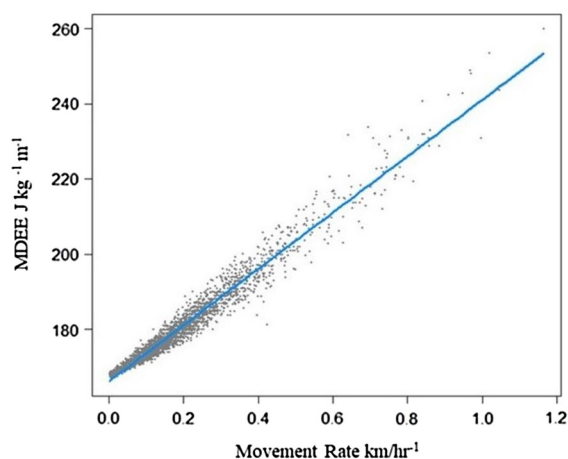


Fig. 4 Relationship between GPS-derived daily movement-based energetic expenditure (MDEE; $\text{J kg}^{-1} \text{m}^{-1}$) and movement rate (km h^{-1} ; parameter estimate = 3.911, $p = 0.001$) for 28 brown bears, Afognak and Sitkalidak islands, Alaska, USA, September 2019–November 2020

measurements, making analysis computationally demanding. A GPS-derived measure of energy expenditure offers an alternative to study animal energetic ecology when accelerometer data may not be available [9, 12]. We compared these two techniques of measuring animal energetics and applied the GPS technique to wild brown bears. We found that GPS-derived estimates of MDEE were on average 1.6 times greater than the ACC method, displayed less overall variation and likely overestimated true energetic expenditure. This finding contrasted with Bryce et al. [9], who noted the energetic costs derived from accelerometers fitted to wolves were on average 1.3 times higher than the GPS method. Discrepancies between our results and that of Bryce et al. [9] may be due to differences in ecology between wolves and brown bears and highlight the importance of species-specific considerations when examining GPS-derived energetic expenditures. It is also important to note that the relationships between oxygen consumption and speed, and oxygen consumption and ODBA in brown bears were devised from a small number of captive animals through two separate studies, and may not fully reflect the energetic demands of free-ranging individuals. Our movement-based energetic expenditures ($2.7\text{--}8.9 \text{ J kg}^{-1} \text{ s}^{-1}$) were similar to ranges reported for brown bears in the Yellowstone ecosystem, with expenditure values of $3.0\text{--}10.6 \text{ J kg}^{-1} \text{ s}^{-1}$ [12]. While energetic costs derived from GPS locations with infrequent resampling should be interpreted with caution, the high correlation between ACC- and GPS-derived estimates of MDEE suggests the GPS technique can be useful to study energetic ecology [12], particularly for providing insights into the energetic

constraints of wild animals. However, this method cannot account for metabolic energy demands and may only be suitable for comparisons of movement-based energy expenditure among individuals [9].

We applied the GPS technique to a larger sample size of wild brown bears on the Kodiak Archipelago and found that bears had greater energy expenditure with increased movement rates and lower energetic expenditure during the high food abundance period, when salmon and berries were abundant. Our strong positive relationship between brown bear movement rate and energetic cost was similar to previous studies [31, 37, 48]. An animal's metabolic rate and speed are fundamentally linked to their dynamic body acceleration [28]. Bears are intrinsically sensitive to increased locomotor speeds due to their plantigrade posture, large body sizes and higher resting metabolic rate compared to similar-sized animals [47]. These higher energetic demands during locomotion may explain why some brown bears, like polar bears (*U. maritimus*), often employ a sit-and-wait predation strategy, particularly along salmon streams [21, 36, 46]. However, this strategy is likely only efficient in areas with access to anadromous salmon. The higher energetic demands associated with increased movement rates may also explain the importance of a social dominance structure among brown bears at prime foraging sites [3, 25]. Certain areas along anadromous fish streams may provide bears the best access to migrating salmon, with reduced costs in obtaining this resource [26]. Under an optimality framework, such locations would be favored due their increased net energy uptake per unit time of effort [27].

Bears had reduced MDEE during the high food abundance period (July–September) when spawning salmon and ripe berries are abundant throughout the Kodiak Archipelago [62]. This finding contradicted our predictions given that bears on the Kodiak Archipelago have larger range sizes during this period [1, 19], and therefore would be expected to experience greater energetic demands associated with locomotion. This reduced MDEE in the high food abundance period supports optimal foraging behavior among brown bears as it suggests that bears minimize energetic cost while maximizing food resource gains in times of increased abundance. Despite traveling greater distances to use resource rich areas, bears reduced energetic costs likely by altering movement and foraging behavior. Brown bears often choose movement paths that offer reduced resistance [12] and can employ sit-and-wait hunting strategies along salmon streams [36]. Such behavioral choices likely attribute to the reduced energetic costs we found in this study.

Our finding of no effect of age and reproductive status on brown bear movement-derived energetic expenditure

was surprising because of previously reported differences in bear movements between males and females, and between younger and older individuals [14, 15]. Larger body sizes incur increased energetic demands, thus species such as brown bears would be expected to have higher energetic costs in older, larger-bodied males [33]. Although we found no such relationship, it is important to note that our energy calculations do not account for internal energetic costs where differences as a result of sex and age may be significant, and our sample of 28 bears included few males which may have limited our ability to detect sex-specific differences. Additionally, as we did not have females with dependent young under the age of 1 year in this study, it may have affected our ability to fully examine how energetic expenditure may have differed between reproductive classes as a result of risk avoidance behavior [3]. We found that lower ambient temperatures were associated with greater energy costs, potentially attributed to the increased thermoregulatory demands on mammals in cooler temperatures [63]. Brown bears may respond to lower temperatures by increasing movements and thus experienced increased energetic costs associated with locomotion. Although, it is also possible that cooler temperatures affected energetics simply due to the time of year that they occurred, as colder temperatures are more common in late fall when food resources are less available, and likely impact bear movements. We found a marginal influence of increased terrain roughness and proximity to salmon streams resulting in higher energetic cost. Large carnivores can be more susceptible to increased costs of movement in mountainous terrain [17]. Although these factors may have influenced bear energetic expenditures, we are cautious to infer such relationships with marginal significance in our GAMM due to the likelihood of model overfitting [73].

Conclusions

The study of animal energetics continues to provide new insights into ecosystem-scale resource requirements, and how animals adapt to spatiotemporal heterogeneous environments [67]. We demonstrated that brown bear movement-based energetic expenditure was sensitive to intrinsic and extrinsic factors, particularly movement rate and food abundance. Human disturbance and alteration of bear habitat may lead to risk-aversion behaviors [38], such as increased movement rates when traversing areas perceived as higher risk [44]. As movement rate increases brown bear cost of transport, such risk avoidance behavior could impede bears from maintaining optimal energetic efficiency. Additionally, as brown bears reduce energetic expenditure when food is abundant, likely by selecting foraging areas with greatest access to

anadromous salmon, increased anthropogenic disturbance at these locations may limit bears from maximizing energetic gain. Such energetic considerations may inform designating areas of high importance for bear conservation and management [67]. We suggest future research examine the GPS method using finer resolution relocation data to improve its accuracy. We also recommend comparisons between methods in a laboratory setting on a larger sample of captive animals. However, as with all studies that involve animal handling, we encourage researchers to consider ethics and animal welfare when designing and implementing energetic ecology research.

Abbreviations

ACC	Accelerometer
GPS	Global positioning system
MDEE	Movement-based daily energetic expenditures
ODBA	Overall dynamic body acceleration
Vo ₂	Rates of oxygen consumption
TRI	Terrain roughness index
GAMMs	Generalized additive mixed models
AICc	Akaike Information Criterion, adjusted for small sample sizes

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00319-0>.

Additional file 1: Table S1. List of 11 a priori models and a null model to assess the influence of internal (reproductive status, age and movement rate), spatial (Terrain roughness, distance from nearest salmon spawning streams), and temporal (food abundance period and temperature) factors on brown bear GPS-derived movement-based energetic expenditure, on the Kodiak Archipelago, Alaska, USA, September 2019–November 2020.

Table S2. Average hourly energetic expenditure ($J\ kg^{-1}\ m^{-1}$) from global position system (GPS) and accelerometer (ACC)-derived estimates for eight brown bears (F = female, FY = female with young, M = male) on the Kodiak Archipelago, Alaska, USA, September 2019–November 2020. (N = number of hourly locations).

Additional file 2. Bear ACC energy data.

Additional file 3. Bear GPS daily energy data.

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Author contributions

SPF, AMP, JLB and NJS conceived the ideas and designed methodology; SPF, JLB, NJS and SLS collected the data; SPF and AMP analyzed the data; SPF led the writing of the manuscript. All authors contributed critically to the drafts. All authors read and approved the final manuscript.

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Availability of data and materials

Data are available upon request from the authors.

Declarations**Ethics approval and consent to participate**

All animal handling procedures were approved by the State University of New York College of Environmental Science and Forestry Institutional Animal Care and Use (IACUC) (protocol 180503) and Alaska Department of Fish and Game (ADFG; IACUC protocol 0030-2017-37).

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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References

- Barnes VG Jr. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. *Bears Biol Manag.* 1990;1:305–13.
- Belant JL, Kielland K, Follmann EH, Adams LG. Interspecific resource partitioning in sympatric ursids. *Ecol Appl.* 2006;16:2333–43.
- Ben-David M, Titus K, Beier LR. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia.* 2004;138:465–74.
- Blanckenhorn WU. The evolution of body size: what keeps organisms small? *Q Rev Biol.* 2000;75:385–407.
- Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP. Observing the unwatchable through acceleration logging of animal behavior. *Anim Biotelem.* 2013;1:1–6.
- Brown DD, LaPoint S, Kays R, Heidrich W, Kummeth F, Wikelski M. Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. *Wildl Soc Bull.* 2012;36:139–46.
- Brownscombe JW, Cooke SJ, Danylchuk AJ. Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia.* 2017;183:689–99.
- Bryce CM, Williams TM. Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds. *J Exp Biol.* 2017;220:312–21.
- Bryce CM, Dunford CE, Pagano AM, Wang Y, Borg BL, Arthur SM, Williams TM. Environmental correlates of activity and energetics in a wide-ranging social carnivore. *Anim Biotelem.* 2022;10:1–6.
- Burnham KP, Anderson DR. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer; 2002.
- Calvert W, Ramsay MA. Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus.* 1998;1:449–53.
- Carnahan AM, van Manen FT, Haroldson MA, Stenhouse GB, Robbins CT. Quantifying energetic costs and defining energy landscapes experienced by grizzly bears. *J Exp Biol.* 2021;224:jeb241083.
- Childs C. Interpolating surfaces in ArcGIS spatial analyst. *ArcUser,* July–Sept. 2004;3235:32–5.
- Dahle B, Swenson JE. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *J Zool.* 2003;260:329–35.
- Dahle B, Støen OG, Swenson JE. Factors influencing home-range size in subadult brown bears. *J Mammal.* 2006;87:859–65.
- Davis ML, Kelly MJ, Stauffer DF. Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. *Anim Conserv.* 2011;14:56–65.
- Dunford CE, Marks NJ, Wilmers CC, Bryce CM, Nickel B, Wolfe LL, Scantlebury DM, Williams TM. Surviving in steep terrain: a lab-to-field assessment of locomotor costs for wild mountain lions (*Puma concolor*). *Mov Ecol.* 2020;8:1–2.
- Ericsson G, Dettki H, Neumann W, Arnemo JM, Singh NJ. Offset between GPS collar-recorded temperature in moose and ambient weather station data. *Eur J Wildl Res.* 2015;61:919–22.
- Finnegan SP, Svoboda NJ, Fowler NL, Schooler SL, Belant JL. Variable intraspecific space use supports optimality in an apex predator. *Sci Rep.* 2021;11:1–3.
- Friebe A, Swenson JE, Sandegren F. Denning chronology of female brown bears in central Sweden. *Ursus.* 2001;12:37–45.
- Garneau DE, Post E, Boudreau T, Keech M, Valkenburg P. Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. *Wildl Biol.* 2007;13:186–94.
- Garshelis DL, McLaughlin CR. Review and evaluation of breakaway devices for bear radiocollars. *Ursus.* 1998;1:459–65.
- Gauthier TD. Detecting trends using Spearman's rank correlation coefficient. *Environ Forensics.* 2001;2:359–62.
- Gehan EA. A generalized Wilcoxon test for comparing arbitrarily singly-censored samples. *Biometrika.* 1965;52:203–24.
- Gende SM, Quinn TP. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Can J Zool.* 2004;82:75–85.
- Gende SM, Quinn TP, Hilborn R, Hendry AP, Dickerson B. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. *Oikos.* 2004;104:518–28.
- Gill ID, Helfield JM. Alternative foraging strategies among bears fishing for salmon: a test of the dominance hypothesis. *Can J Zool.* 2012;90:766–75.
- Gleiss AC, Wilson RP, Shepard EL. Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol Evol.* 2011;2:23–33.
- Green JA. The heart rate method for estimating metabolic rate: review and recommendations. *Comp Biochem Physiol A: Mol Integr Physiol.* 2011;158:287–304.
- Halsey LG, Bryce CM. Proxy problems: why a calibration is essential for interpreting quantified changes in energy expenditure from logging data. *Funct Ecol.* 2021;35:627–34.
- Halsey LG, White CR. Comparative energetics of mammalian locomotion: humans are not different. *J Hum Evol.* 2012;63:718–22.
- Hilderbrand GV, Gustine DD, Mangipane BA, Joly K, Leacock W, Mangipane LS, Erlenbach J, Sorum MS, Cameron MD, Belant JL, Cambier T. Body size and lean mass of brown bears across and within four diverse ecosystems. *J Zool.* 2018;305:53–62.
- Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can J Zool.* 1999;77:132–8.
- Hollister J, Shah T, Robitaille A, Beck M, Johnson M. elevatr: access elevation data from various APIs. R package version 0.4.2. 2021.
- Karasov WH. Daily energy expenditure and the cost of activity in mammals. *Am Zool.* 1992;32:238–48.
- Klinka DR, Reimchen TE. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Can J Zool.* 2002;80:1317–22.
- Maloji GM, Rugangazi BM, Rowe MF. Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. *J Zool.* 2009;277:248–55.
- Martin J, Basille M, Van Moorter B, Kindberg J, Allaine D, Swenson JE. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Can J Zool.* 2010;88:875–83.
- Masello JF, Barbosa A, Kato A, Mattern T, Medeiros R, Stockdale JE, Kümmel MN, Bustamante P, Belliure J, Benzal J, Colominas-Ciuró R. How animals distribute themselves in space: energy landscapes of Antarctic avian predators. *Mov Ecol.* 2021;9:1–25.
- Masello JF, Kato A, Sommerfeld J, Mattern T, Quillfeldt P. How animals distribute themselves in space: variable energy landscapes. *Front Zool.* 2017;14:1–4.
- McDonough TJ, Christ AM. Geographic variation in size, growth, and sexual dimorphism of Alaska brown bears, *Ursus arctos*. *J Mammal.* 2012;93:686–97.
- McNab BK. Bioenergetics and the determination of home range size. *Am Nat.* 1963;97:133–40.

43. Munro RHM, Nielsen SE, Price MH, Stenhouse GB, Boyce MS. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *J Mammal*. 2006;87:1112–21.
44. Ordiz A, Støen OG, Sæbø S, Sahlén V, Pedersen BE, Kindberg J, Swenson JE. Lasting behavioural responses of brown bears to experimental encounters with humans. *J Appl Ecol*. 2013;50:306–14.
45. Pagano AM, Atwood TC, Durner GM, Williams TM. The seasonal energetic landscape of an apex marine carnivore, the polar bear. *Ecology*. 2020;101:3.
46. Pagano AM, Carnahan AM, Robbins CT, Owen MA, Batson T, Wagner N, Cutting A, Nicassio-Hiskey N, Hash A, Williams TM. Energetic costs of locomotion in bears: is plantigrade locomotion energetically economical? *J Exp Biol*. 2018;221:12.
47. Pagano AM, Durner GM, Rode KD, Atwood TC, Atkinson SN, Peacock E, Costa DP, Owen MA, Williams TM. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science*. 2018;359:568–72.
48. Pagano AM, Williams TM. Estimating the energy expenditure of free-ranging polar bears using tri-axial accelerometers: a validation with doubly labeled water. *Ecol Evol*. 2019;7:4210–9.
49. Pyke GH, Pulliam HR, Charnov EL. Optimal foraging: a selective review of theory and tests. *Q Rev Biol*. 1977;52:137–54.
50. Pyle B, Hernandez D. Development of protocols for monitoring phenology and abundance of berries important to brown bear in the Kodiak Archipelago, Alaska. Kodiak: US Fish and Wildlife Service, Kodiak National Wildlife Refuge; 2017.
51. R Foundation for Statistical Computing. R: a language and environment for statistical computing. 2020. <http://www.r-project.org/>.
52. Riley SJ, DeGloria SD, Elliot R. Index that quantifies topographic heterogeneity. *Intermt J Sci*. 1999;5:23–7.
53. Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. Energy landscapes shape animal movement ecology. *Am Nat*. 2013;182:298–312.
54. Shepard EL, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C. Identification of animal movement patterns using tri-axial accelerometry. *Endanger Species Res*. 2008;10:47–60.
55. Smith MW. Roughness in the earth sciences. *Earth Sci Rev*. 2014;136:202–25.
56. Steudel KA. The physiology and energetics of movement: effects on individuals and groups. On the move: how and why animals travel in groups. Chicago: University of Chicago Press; 2000.
57. Stirling I, Spencer C, Andriashek D. Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. *J Wildl Dis*. 1989;25:159–68.
58. Swenson JE, Adamič M, Huber D, Stokke S. Brown bear body mass and growth in northern and southern Europe. *Oecologia*. 2007;153:37–47.
59. Swenson JE, Dahle B, Sandegren F. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus*. 2001;12:81–91.
60. Thiemann GW, Derocher AE, Cherry SG, Lunn NJ, Peacock E, Sahanatien V. Effects of chemical immobilization on the movement rates of free-ranging polar bears. *J Mammal*. 2013;94:386–97.
61. Thomas B, Holland JD, Minot EO. Wildlife tracking technology options and cost considerations. *Wildl Res*. 2011;38:653–63.
62. Van Daele LJ, Barnes VG, Belant JL. Ecological flexibility of brown bears on Kodiak Island, Alaska. *Ursus*. 2012;23:21–9.
63. Walcott SM, Kirkham AL, Burns JM. Thermoregulatory costs in molting Antarctic Weddell seals: impacts of physiological and environmental conditions. *Conserv Physiol*. 2020;8:1.
64. Weibel ER, Bacigalupe LD, Schmitt B, Hoppeler H. Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir Physiol Neurobiol*. 2004;140:115–32.
65. Westerterp KR. Doubly labelled water assessment of energy expenditure: principle, practice, and promise. *Eur J Appl Physiol*. 2017;117:1277–85.
66. Williams TM, Wolfe L, Davis T, Kendall T, Richter B, Wang Y, Bryce C, Elkaim GH, Wilmers CC. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science*. 2014;346:81–5.
67. Williams TM, Peter-Heide Jørgensen M, Pagano AM, Bryce CM. Hunters versus hunted: new perspectives on the energetic costs of survival at the top of the food chain. *Funct Ecol*. 2020;10:2015–29.
68. Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R, Hopkins L. Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. *J Anim Ecol*. 2020;89:161–72.
69. Wilson RP, Quintana F, Hobson VJ. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc R Soc B: Biol Sci*. 2012;279:975–80.
70. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol*. 2006;75:1081–90.
71. Wood SN. Generalized additive models: an introduction with R. 1st ed. New York: Chapman and Hall/CRC Press; 2006. <https://doi.org/10.1201/9781420010404>.
72. Wood SN. mgcv: GAMs and generalized ridge regression for R. *R news*. 2001;1:20–5.
73. Wood SN. On p-values for smooth components of an extended generalized additive model. *Biometrika*. 2013;100:221–8.
74. Young RL, Weinberg J, Vieira V, Ozonoff A, Webster TF. Generalized additive models and inflated type I error rates of smoother significance tests. *Comput Stat Data Anal*. 2011;55:366–74.

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