A winter energetics model for bobcats in a deep snow environment

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A B S T R A C T

Understanding basic energetic requirements of wildlife species is critical to evaluate how individuals persist in their current environments as well as to forecast responses to changed climates or habitats. Indeed, northern range limits are often thought to reflect harsh abiotic conditions that exceed the capacity of individuals to stay in energetic balance. Bobcats (*Lynx rufus*) occur across much of North America; at northern latitudes, they face winter challenges such as deep snows, cold temperatures, and possible food scarcity. We developed an energetics model from field data on movements, body mass, and observed diet of bobcats in mountains of northwest Montana, then evaluated overwinter prey requirements that would enable bobcats to stay in energy balance in this difficult environment. Our model indicated average daily energy expenditures were $\sim 1.41\times$ basal metabolic rate. For 90 days from December to February, a 10.5 kg bobcat consuming prey items in proportion with the observed diet for bobcats in this area would need about 2.1 kg of deer (*Odocoileus* spp.), 7 snowshoe hares (*Lepus americanus*), 155 red squirrels (*Tamiasciurus hudsonicus*), 9 woodrats (*Neotoma cinerea*), and 250 small rodents (Cricetidae). Bobcats have considerable flexibility in diet, movements, and both timing and duration of daily activity to adjust their energetic expenditures in winter.

1. Introduction

Understanding the basic energetic requirements of individuals allows ecologists to determine how well suited an animal is to a given landscape (Laundré, 2005) as well as to gauge possible causes of range limits. Winter in northern latitudes presents individual animals with many challenges, including snow, cold temperatures, and food scarcity (e.g. Hodges et al., 2006). Animals can deal with harsh conditions through behavioral and physiological adaptations (Kingsolver and Huey, 1998). Physiological adaptations include hibernation, increases in body fat, reduced metabolic rates, and increases in fur length and density (Williams et al., 2015). Behavioral responses to challenging winter conditions vary substantially among individuals or in differing local conditions. Common behavioral changes include reducing movements, changing hunting techniques (e.g. ambush vs. stalking), changing quantity or quality of prey consumed, changing nocturnal or diurnal movement patterns, ceasing movements during extreme weather, and selecting microhabitats that provide temperature refugia or sunlight for basking (Williams et al., 2015)

For carnivores that have broad geographic ranges, a key question is how they manage in the most extreme environments, which often occur at northern or high elevation range peripheries. Such environments are likely more challenging energetically than conditions individuals experience in the core of their geographic distribution. Further, the prey base may be more limited in such environments than in areas without prolonged and cold winters. In this paper, we examine the winter energetics of bobcats (*Lynx rufus*), common North American felids that are habitat and prey generalists.

Bobcats are widely distributed throughout the United States, but are less common in southern Canada where they may be limited by environmental conditions, particularly deep snow and cold temperatures (Koehler and Hornocker, 1989; Litvaitis et al., 1986a, 1986b; Major, 1983; Matlack and Evans, 1992). Bobcats reduce movements in winter (Apps, 1996; Koehler and Hornocker, 1989), and in some locations bobcats contract their winter home range sizes or use habitats that provide snow-free access to prey (Bailey, 1974; Koehler and Hornocker, 1989). In regions where all habitats have snow during winter, bobcats are expected to expend higher amounts of energy overwinter than in regions where some habitats remain snow-free. In northwest Montana, bobcats live in an environment that is characterized by cold winter temperatures and deep, persistent snows. Although previous work on bobcats has shown that metabolic rate is higher in winter (Mautz and Pekins, 1989), and that different prey offer different metabolizable energy (Powers et al., 1989), models have not yet integrated data on bobcats' winter movements, diet, and daily energy expenditure in such harsh conditions.

Our ultimate objective in this paper is to develop an energetics model for bobcats in the winter conditions of northwestern Montana. Our specific goals are three-fold: (1) to develop a realistic model of a bobcat's energy requirements in this snowy winter environment; (2) to examine whether bobcats in northwest Montana are able to meet the estimated daily energy expenditures on the diets they obtain, and (3) to explore the behavioral strategies bobcats can use to offset caloric expenditures from potential thermoregulatory requirements and the high energetic cost of moving in deep snow conditions.

2. Materials and methods

2.1. Study area

We worked in the Salish Mountains of northwest Montana, a region that encompassed ~ 10,700 km^2 with > 30 peaks over 1828 m, 10 of which were located in the study area. Additionally, there were > 30 peaks between 1524 and 1828 m, many of which were located on the study area where bobcats were radiocollared. The Tally Lake Ranger District of the Flathead National Forest, Montana, USA (48°30′0″N, 114°45′0″W), was located in the center of the Salish Range, with elevations between 945 m and 2008 m. Winter temperatures ranged from − 42 to 7 °C (NOAA, 2013), and average winter snowfall was > 3 m at mid-elevations (~ 1300–1650 m), with > 7 m of snowfall above 2000 m (NOAA, 2013).

The study area was dominated by moist coniferous forests of western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Lodgepole pine forests formed 30% of the landscape and an additional 30% was formed by Douglas fir and larch associations. Subalpine fir forests constituted 20% of the area. Other trees in the region included Ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), whitebark pine (*Pinus albicaulis*), and subalpine larch (*Larix lyallii*) (Flathead National Forest, 2006).

The available prey were snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), grouse (*Falcipennis canadensis* and *Bonasa umbellus*), bushy-tailed woodrats (*Neotoma cinerea*), a variety of small mammals (mice and voles, Neotominae and Arvicolinae), and carrion. Deer (*Odocoileus virginianus* and *O. hemionus*) were uncommon at high elevations in winter, but they and moose (*Alces americana*) could have provided carrion.

2.2. Field methods

We trapped bobcats during winters 2008–2011 in commercially available box traps (Havahart) or box traps we constructed (Kolbe et al., 2003). We baited traps with road-killed deer, commercially available scent lures (Bob Wilson's lures, Murray's brand, Murray's Lures & Trapping Supplies), and a CD on fishing line as a visual lure.

We used an extendable pole-syringe to immobilize bobcats with Telazol® at 5 mg/kg estimated body mass. Bobcats were sexed, weighed, and ear-tagged (National Band and Tag Co., 1005-4 Monel, sequential numbering). We fitted each bobcat weighing > 4 kg with a Lotek GPS_3300SL (Lotek Eng. Inc., Newmarket, ON) or Sirtrack Model TGC181 GPS/VHF satellite telemetry collar (Sirtrack®, Hawkes Bay, New Zealand); each collar was < 5% of the bobcat's body mass. We released bobcats at the point of capture. Collars obtained high accuracy locations (± 4 m) every 3 h. We retrieved collars either after animals died or via re-trapping. Collars were equipped with a collar release mechanism with a scheduled collar drop date; however, all collars failed to release properly, necessitating trapping to retrieve radio-collars. Live-trapping was permitted by Montana State Fish, Wildlife, and Parks (2009-059, 2010-002, 2011-003), and the University of British Columbia's Animal Care Committee (A07-0676-R001); our work adhered to the guidelines of the American Society of Mammalogists (Sikes et al., 2016).

2.3. Winter energetics model for bobcats

For this model, we used the same framework as Aldama et al.'s (1991) Iberian lynx (*Lynx pardinus*) energetics model, which was based on Powell's (1979) fisher (*Pekania pennanti*) energetics model. Total energetic cost (C_T, or Daily Energetic Expenditure, DEE) for non-reproductive animals is defined as:

$$C_T = C_{th} + C_r + C_l + C_h + C_e \tag{1}$$

The costs of thermoregulation (C_{th}), resting (C_r), locomotion (C_l), hunting (C_h), and eating (C_e) are defined below.

(1) Cost of thermoregulation (C_{th}). We dropped this term from our model for two reasons. First, we are aware of only one data-based estimate for the lower critical temperature (T_{lc} = − 2.2 °C) at which bobcats would begin to thermoregulate (Mautz and Pekins, 1989). We think this estimate is unreasonably high for our population. This estimate was derived from 4 individual eastern bobcats kept in small cages, not reflecting free-living western bobcats acclimated to local winter conditions. Eastern and western bobcats show strong genetic separation that arose during the Pleistocene (Croteau et al., 2012; Reding et al., 2012), further suggesting that this T_{lc} from eastern bobcats is inappropriate for a different genetic group. Similarly, the bobcats in our study area are from the largest subspecies (*L. rufus pallescens*), again suggesting there may be physiological differences.

Second, Powell's (1979) estimate of daily energy expenditures for fishers directly relates T_{lc} and underfur length for several cold-adapted mesocarnivores; species with long fur have much lower critical temperatures. Fishers have underfur length 2.1 ± 0.2 cm (± S.D.), leading to a best estimate of T_{lc} of − 30 to − 20 °C for active fishers, and − 80 to − 40 °C for a sleeping fisher curled in a ball in microhabitat refugium. Bobcat guard hairs range from 4.5 cm (Moore et al., 1974) to 6.6 cm (Harrison, 2002); Linawang et al. (2012) report bobcat underfur (n = 2 samples) is 1.4 cm long with a density of 48.1 hairs/mm, a density above that of polar bears (*Ursus maritimus*); unfortunately, these authors do not specify whether they sampled from western or eastern bobcats, nor is it clear how much the length of bobcat underfur varies seasonally. Eurasian lynx (*L. lynx*) have guard hair length of 5.1 cm and underfur length of 3.1 cm, while snow leopards (*Panthera uncia*) have guard hairs 5.4 cm and underfur 4.3 cm (Heptner and Sludskii, 1992). Although the very limited sample of bobcat underfur suggests it is shorter than that of these other felids, the high underfur density and long guard hairs likely contribute to high insulative value.

Thus, we assume that T_{lc} for bobcats is substantially lower than the − 2.2 °C Mautz and Pekins (1989) derived for eastern bobcats. When C_{th} is dropped from Eq. (1), the equation becomes:

$$C_T = C_r + C_l + C_h + C_e \tag{2}$$

(2) Cost of resting (C_r). We follow typical models and calculate the basal metabolic rate as $C_r = 70 \times W^{0.75}$ kcal/day, where W is mass in kg (Aldama et al., 1991). To account for time engaged in other activities, we calculated time spent resting as $C_r = (70 \times W^{0.75}$ kcal$)\left(\frac{24\,h - t_2 - t_3 - t_4}{24\,h}\right)$, where t_2 is time spent active, t_3 is time spent hunting, and t_4 is time spent eating.

(3) Cost of locomotion, $C_l = 5.8 \times W^{0.75} \times t_2 + 2.6 \times W^{0.6} \times d$, where t_2 is time spent in motion (walking, foraging, territorial marking), and d is daily distance travelled in km (Taylor et al., 1970). This formula assumes constant effort and speed, but is standard in the energetics

literature (Aldama et al., 1991; Laundré, 2005; Powell, 1979). Crête and Larivière (2003) document that changing travel speed from 1 km/h to 5 km/h increased the heart rate of domestic dogs (used as a proxy for coyotes, *Canis latrans*) by up to 20%, but they also note that coyotes typically travel at speeds around 1 km/h. Bobcats in more southern localities typically move at speeds of < 1 km/h (Elizalde-Arellano et al., 2012). Finally, based on our field observations, bobcats typically walk rather than trot or run in snow, so we do not include high energetic costs for fast gaits. Searching for prey would be included in this cost.

(4) Cost of prey capture (hereafter, "hunting"), $C_h = 78.3 \times W^{0.84} \times t_3$, where t_3 is the time spent chasing, attacking, and subduing prey (Calder, 1984). We expect this value is an over-estimate for bobcats, because the majority of the prey they eat in this system are small rodents (Newbury and Hodges, 2018) that are killed with one leap and bite.

(5) Cost of eating, $C_e = (5.8 \times W^{0.75} + 3.12 \times W^{0.6}) \times t_4$, where t_4 is time spent eating (Ackerman et al., 1986).

Inserting all terms into Eq. (2), daily energy expenditure becomes:

$$C_T = (70 \times W^{0.75} \text{ kcal}) \times \left(\frac{24 \text{ h} - t_2 - t_3 - t_4}{24 \text{ h}} \right)$$
$$+ (5.8 \times W^{0.75} \times t_2 + 2.6 \times W^{0.6} \times d) + 78.3 \times W^{0.84} \times t_3)$$
$$+ ((5.8 \times W^{0.75} + 3.12 \times W^{0.6}) \times t_4) \tag{3}$$

2.3.1. Model development

We first calculated basal metabolic rate (C_r) for bobcats ranging from 5 to 15 kg. We then calculated Daily Energy Expenditure (DEE) using a range of realistic parameter combinations to determine daily caloric needs. We developed a Baseline Winter Activity scenario by selecting high but possible values for movement, activity, hunting, and eating, reflecting our field data as much as possible. We deliberately wanted this scenario to be more likely to overestimate than underestimate average daily energy expenditures, especially since our field-based estimates of movement may be slightly underestimated because fixes were obtained every 3 h. This Baseline scenario is useful both as a point of contrast for other scenarios, and as our best estimate of energetic needs across the entire winter. We then developed 6 other possible daily scenarios, ranging from an inactive bobcat (simulates C_r and a bobcat that stays inactive during a winter storm or cold snap) to a highly active bobcat (Table 1). These scenarios likely bracket the extremes for C_T. We examined C_T under all 7 scenarios for bobcats weighing 5–15 kg.

We then examined how total energetic cost (C_T) varied with different scenarios for movement, activity, hunting, and eating (Table 1). We used the Baseline Winter Activity scenario, then individually varied each parameter across a realistic range of possible values. This sensitivity testing is reasonably realistic for time spent eating (varied from 0.25 to 4.5 h) and time spent hunting (varied from 2 min to 2 h). For distance travelled and total time spent active, the sensitivities are more

artificial because for a real bobcat these parameters would almost certainly covary, whereas here we kept distance moved at 5 km while allowing activity time to vary from 0 to 18 h, and conversely we kept activity at 4 h while allowing distance travelled to vary from 0 to 20 km. These probes still signal how much impact the individual variable has on energetic demands, but they are less likely to simulate a genuine bobcat-day; the seven scenarios reflect actual bobcat-days better.

2.3.2. Parameterizing the model: bobcat movements and activities

Whenever possible, we parameterized the energetics scenarios from the field data we obtained in Montana (Table 2, Newbury, 2013). We used masses and daily distances moved of radiocollared bobcats. Daily distances moved by each bobcat were determined by summing straight line distances between consecutive UTM coordinates for an individual. Summed distances were divided by the number of days in winter, or the number of days that the bobcat was radiocollared in that season, to obtain standardized distance per 24 h. Bobcats displayed roughly linear movements, as we observed when we were backtracking individual animals via snow tracks to assess fine scale habitat selection patterns (Newbury, 2013). We believe the 3-hr fixes captures these movements in a relatively faithful manner, as bobcats did not appear to circuitously search areas. We acknowledge that total movement distances may be slightly underestimated but not enough to significantly impact outcomes of this mathematical model. We used meteorological winter, i.e. the 90 days from 1 December to 28 February. All bobcats had < 90 radiocollared days in winter, as they were collared either after December 1 or the radiocollar failed before the end of winter.

We also deliberately built some scenarios with very high movement distances of bobcats throughout the winter (Table 1). Scenarios 5–7 used movement distances of ≥ 5 km moved per day, which are credible for various *Lynx* sp. Maximum movements reported for Iberian lynx were 11.1 km daily (Aldama et al., 1991). Canada lynx (*Lynx canadensis*) have daily movements of 7 km (Moen et al., 2008), 8.8 km (Parker et al., 1983), and 23.3 km (Apps, 2000). During winter, bobcats have moved 11.7 km (Erickson, 1955), 11.2 km (Rollings, 1945), 8 km (Bailey, 1974), and 8.7 km per day (Sullivan, 1995). In contrast to these estimates of maximum distances, Bailey (1974) worked in an arid study area in Idaho, and reported that the majority of male bobcats moved < 4.8 km/day in winter, and females typically moved < 3.2 km/day. Elizalde-Arellano et al. (2012) summarize studies of bobcats from their southern range, where winter snow is far less common, and in all cases average daily movements were < 9 km, with an over-all average of 5.7 km/day. We explored scenarios that ranged from 0 to 20 km of daily movement.

Average time spent active was difficult to estimate from GPS collar data due to the programmed duty cycle of one location every 3 h. We therefore used scenarios that varied from 0 to 20 h of daily activity. Bobcats are primarily crepuscular (Elizalde-Arellano et al., 2012; Rockhill et al., 2013; Leonard, 2016), although often with some nocturnal activity as well. Calculations of energy expenditures based on

Table 1
Activity scenarios used as examples for daily energy expenditure by bobcats in winter, presented from lowest to highest energy expenditures. All times are in hours. In Scenario 7, Extreme Activity, the bobcat is assumed to be active 24 h, with no time spent resting. All other scenarios assume that the bobcat is resting when not engaged in activity; for example, in Scenario 6, High Activity, the bobcat is assumed to be resting 3.5 h, while in Scenario 1, Basal Metabolic Rate (C_r), the bobcat rests for the entire 24 h.

Scenario	Distance moved in 24 h (km)	Time spent active	Time spent hunting	Time spent eating
1. Basal Metabolic Rate	0	0	0	0
2. Very Low Activity	1	1	0.008 (30 s)	0.1 (6 min)
3. Low Activity	3	2	0.017 (1 min)	0.5 (30 min)
4. Baseline Winter Activity	5	4	0.033 (2 min)	1
5. Medium-high Activity	10	10	0.083 (5 min)	2
6. High Activity	15	16	1	3.5
7. Extreme Activity	20	17.5	2	4.5

Table 2

Mass and daily winter movement distances of four radiocollared bobcats in northwest Montana. Male bobcats are indicated by "M", while the female bobcat is "F2". Values are means ± 1 SD. Daily energy expenditures were calculated from actual distances moved, with time spent active, hunting, and eating held constant as in the Baseline Winter Activity scenario.

Bobcat ID	Mass (kg)	Average daily movement (km)	Range of daily movement (km)	Average Daily Energy Expenditure (kcal)	Range of Daily Energy Expenditure (kcal)
M1	14	4.42 ± 3.01	0.06–16.3	705 ± 4.1	649–856
M2	9.5	2.15 ± 1.54	0.13–6.1	507 ± 2.8	487–546
M3	14.5	2.75 ± 2.48	0.78–5.6	702 ± 18.5	677–738
F2	11	2.21 ± 1.68	0.20–4.9	566 ± 5.8	544–596

daily activity of > 10 h may be unrealistic for most bobcats given clear patterns showing little diurnal activity, though diurnal activity has been documented (e.g. Newbury, 2013, Rockhill et al., 2013, Leonard, 2016).

We varied time spent hunting from 0 to 2 h; 2 h represents an extreme and unlikely estimate. An average time spent hunting of 2 min was based upon the convention of a wild Iberian lynx chasing a hare for 30 s (Aldama et al., 1991). With an average hunting success of 25%, 4 hunting attempts are required before prey is captured such that 30 s × 4 attempts = 2 min. Hunting success of 25% is well within the range of hunting success of 9–36% and 14–55% estimated for Canada lynx (Brand et al., 1976; Parker et al., 1983), so we think bobcats hunting hares would similarly spend ≤ 30 s per attempt. Bobcats in our study area ate many small rodents and red squirrels (*Tamiasciurus hudsonicus*; Newbury and Hodges, 2018), and these prey would likely take substantially less time to hunt and to consume than would snowshoe hares. Time spent eating prey was varied from 0 to 4.5 h, with an average time spent consuming prey of 1 h based upon estimates of time spent eating by captive Iberian lynx (Aldama et al., 1991).

2.3.3. Winter prey requirements for energetic balance

We based daily and overwinter prey requirements on the observed diet of bobcats in northwest Montana (Table 3, Newbury and Hodges, 2018). Grouse were < 1% of the diet, so we excluded grouse from our calculations here. For the other prey types, we calculated energy obtained from each prey type from estimates of gross energy intake by bobcats (Powers et al., 1989). C_T of bobcats were then divided by metabolizable kcal obtained from each species to determine how many of each prey type would be required if a bobcat ate prey proportionally to this observed distribution.

3. Results

We radiocollared eight bobcats (6 M, 2 F); additionally, 1 M and 1 F were captured but not fitted with collars. Collars from 4 males and 1 female were recovered, with 7664 total GPS locations, of which 692

Fig. 1. Total energetic cost (C_T) in relation to bobcat mass predicted by the daily energetics model for various activity levels (Scenarios 1–7) in winter in northwest Montana.

were obtained during winter (17–426 locations per individual in winter); 1 male was collared in March, and his collar failed by late June, yielding no useable winter movement data. The body masses of male bobcats ranged from 4.5 to 15 kg, and female bobcats weighed 7.75–11 kg (Table 2); the average mass of all 8 bobcats was 10.5 kg, so we use this value as our primary example.

A 10.5 kg bobcat engaged in the activity levels of the Basal Winter Activity scenario would expend 577 kcal per day, or 1.41 × C_r (Table 1, Fig. 1, Scenario 4). If this cat instead simply rested all day (C_r, Scenario 1), it would use 408 kcal per day. Our most energetically demanding scenario (#7), would require the bobcat to expend 2144 kcal/day, a rate of 5.25 × C_r.

The majority of bobcat daily movements were ≤ 6 km (114 of 138, 82.6%). Of the days when bobcats travelled more than 6 km, 19 of the 24 days had movements ≤ 9 km (Fig. 2). If we use the Baseline Winter Activity scenario, a 10.5 kg bobcat moving 10 km would expend 630 kcal vs. 577 kcal for 5 km. If we jointly increase time active to 8 h

Table 3

Energy obtained by bobcats from prey types available in northwest Montana. The % biomass of prey in the diet reflect diets of bobcats in northwestern Montana (Newbury and Hodges, 2018); nutritional values are taken from the literature.

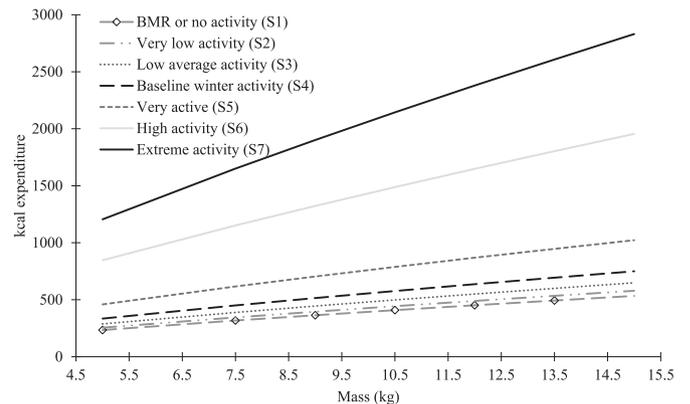| Species	% biomass consumed	mass (kg)	Dry matter content[a] %	Digestible energy[a] (kcal/g)	Metabolizable energy %[a]	kcal obtained	Number[c] needed/day by a 10.5 kg bobcat
Squirrel	54.0	0.195	25.9	4.8	74.9	181.6	1.70
Cricetidae[d]	19.3	0.038	33.3	4.43	71.6	40.1	2.8
Woodrat[e]	5.2	0.336	25.9	4.8	74.9	312.9	0.1
Snowshoe hare	12.2	1.4	29.7	3.61	62.7	941.2	0.1
Deer[f]	8.5	60	39.0	6.25	85.8	2091.4[b]	~ 23 g

[a] From Powers et al. (1989).
[b] Assumes that a bobcat consumes 1 kg of deer during a feeding.
[c] Required to satisfy C_T of 577 kcal/day for a 10.5 kg bobcat as calculated from the Baseline Winter Activity scenario.
[d] Not including woodrats.
[e] As dry matter content, digestible energy, and metabolizable energy have not been computed for bobcats consuming woodrats, we assumed that these parameters would be comparable to a red squirrel.
[f] Deer consumed is presented in amount needed to satisfy caloric requirements from the observed diet. Deer was 8.5% biomass of observed diet, which equals 49.0 kcal or 23 g of deer per day. All other numbers are presented in whole animal counts.
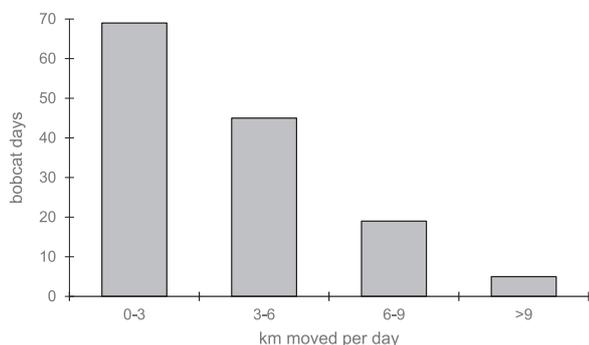
Fig. 2. Distance moved per day by bobcats in winter in northwest Montana. Data reflect 138 bobcat-days obtained from 4 radio-collared bobcats during winters 2008–2011.

(instead of the baseline 4) then the bobcat would need 644 kcal/day. At the extreme, we observed one male moving 16.3 km in a 24 h period, but we do not know how many hours he was active that day. Using the mean winter movements of radiocollared males (= 3.1 km) and female bobcats (= 2.2 km), and holding other parameters as in the Baseline Winter Activity scenario, males had C_T of 517–707 kcal, and females had C_T of 544–596 kcal (Table 2).

The estimated C_T was by far the most sensitive to time hunting, as the cost of attacking and subduing prey is high (Fig. 3). For example, with Baseline Winter Activity parameters, and varying terms individually, if a 10.5 kg bobcat spent 1 h moving or 1 h eating, it expended only 526 or 576 kcal/day respectively, but if it spent 1 h hunting, then it expended 1105 kcal/day. Unsurprisingly, heavier bobcats required more kcal/day for any given duration of an activity; for 1 h of hunting a 15 kg bobcat would expend 1465 kcal/day, compared to only 617 kcal/day for a 5 kg bobcat.
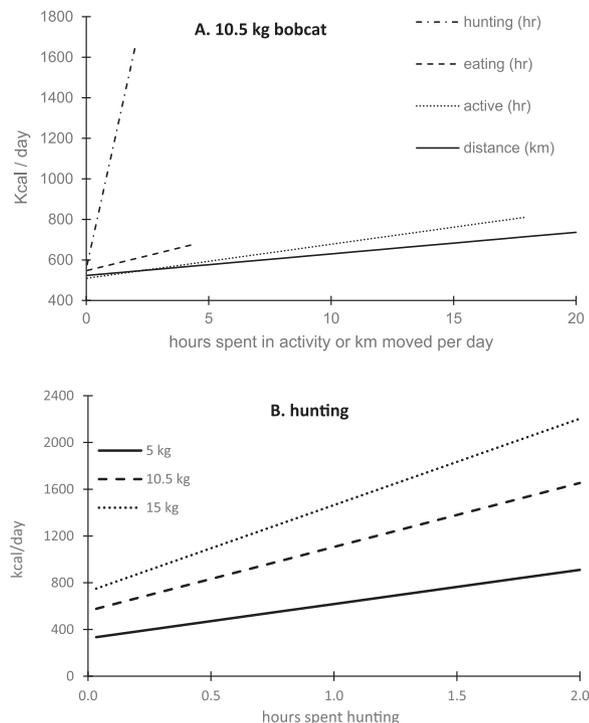
Fig. 3. Daily energetic costs for bobcats in relation to model inputs. We used the Baseline Winter Activity scenario, then varied each input individually across a credible range. A) Daily energetic cost for hunting, eating, activity, and distance moved as functions of hours spent or km moved for a 10.5 kg bobcat. The lines are truncated at extremely high durations or distances for each input. B) Daily energetic cost as a function of body mass and hours spent hunting.
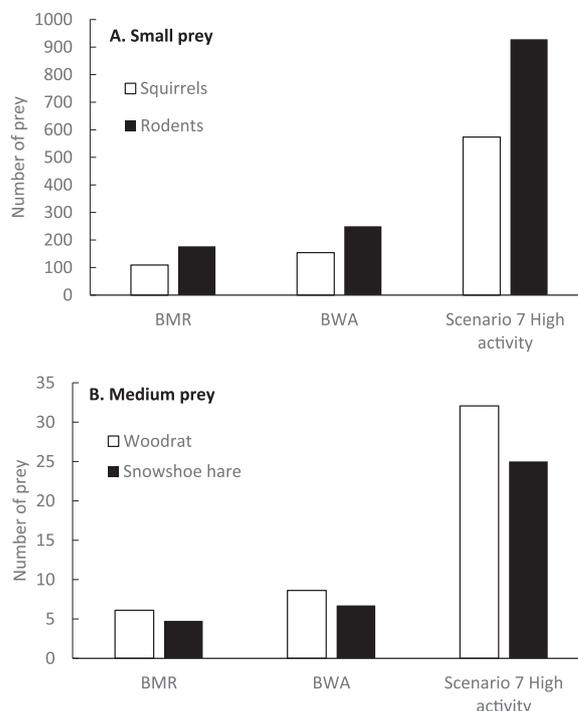
Fig. 4. Overwinter (90 day) prey requirements for a 10.5 kg bobcat consuming the observed winter diet of northwest Montana bobcats (Newbury and Hodges, 2018). We compare no activity (C_r), the Baseline Winter Activity scenario, and extremely high activity. Note different y-axes. Consumption of deer is not shown, but likely would have been consumed as carrion, or multiple meals from one hunt.

3.1. Overwinter prey requirements for bobcats

Elsewhere, we have documented the winter diet of bobcats in this region (Newbury, 2013; Newbury and Hodges, 2018). If we assume that bobcats eat in proportion to this diet and calculate their prey needs based on the energy obtainable from these prey types then the daily diet of a 10.5 kg bobcat in northwest Montana expending the energy from the baseline winter scenario would consist of 1.7 squirrels, 0.1 woodrats, 2.7 small rodents, 0.07 snowshoe hares, and ~ 23 g of deer (Table 3). The Baseline Winter Activity scenario results in an energy expenditure of 51,889 kcal from December to February. Overwinter, a 10.5 kg bobcat would need to consume approximately 155 squirrels and 250 small rodents (Fig. 4a), 7 snowshoe hares, 9 woodrats (Fig. 4b), and 2.1 kg of deer to remain in energy balance through winter. If bobcats were instead extremely active, these prey needs would increase substantively (Fig. 4).

4. Discussion

We have developed a model for the winter energetics of bobcats in northwestern Montana. In our scenario designed to reflect typical costs, we deliberately overestimated daily movements and activity, preferring to err on the side of overestimating average energetic needs than underestimating them. Specifically, our Baseline Winter scenario assumed 5 km/day, but male bobcats in our study moved on average 3.1 km/day, while the radio-collared female bobcat moved an average of 2.2 km/day. We then assessed in more detail just how costly it would be to be a very active bobcat in winter versus an energy-conserving one.

Our scenarios were built to cover even long movement distances that derive from bobcats in ecosystems with far less snow, but only 4% of bobcat-days in our study area had movements > 9 km. Of 138 bobcat-days, 50% of movements were ≤ 3 km, with over 80% of all daily movements ≤ 6 km. Our telemetry locations were taken every 3 h.

Based on our familiarity with tracks of bobcats in the area, net displacement per 3 h is likely a modest underestimate of true distances moved, but not a severe one. Bobcats navigated their landscape in a roughly linear fashion and typically walked rather than trotting or running (Newbury, 2013)

One male bobcat in our study exceeded the Baseline Winter Activity movement distance of 5 km for 38 of 87 days (43.7%) in a single winter, including one 24-h period during which he moved 16.3 km (Table 2). Despite his many high-activity days, he still averaged only 4.4 km/day across winter, well below the 5 km we used in the Baseline Winter Activity scenario. The Low Average Activity scenario (Table 1; 3 km daily) was more typical for the < 3 km average daily movements of the other bobcats; using this scenario, C_T requirements for a 10.5 kg bobcat drop by 16% from 577 kcal to 498 kcal. We note these lower values are quite similar to estimates from Aldama et al. (1991) for Iberian lynx; these authors also did not model thermoregulation, and they estimated a 9.95 kg female would need 673 kcal (554 kcal this study at Baseline Winter Activity) and a 15.4 kg male would need 914 kcal (764 kcal this study) per day. The difference in estimated daily energy requirements between Aldama et al. (1991) and our results is at least partially explained by the higher daily average distances they modeled.

The energetics model is extremely sensitive to minor changes in time spent hunting (Fig. 3). This parameter includes the costs of chasing, capturing, and killing prey (Calder, 1984). This high energetic cost is almost certainly over-estimated for bobcats, as 80% of their diet in this region consists of prey < 1 kg (Newbury and Hodges, 2018). For example, a bobcat killing a small rodent usually does so with one pounce (Hamilton and Hunter, 1939); no chase is required and there is essentially no cost for subduing the prey. The costs of moving through a home range and watching for prey en route are included in the time spent active and the locomotion terms of this model. Our scenarios show that moving longer distances, even when coupled to longer times spent active, are not nearly as energetically demanding as even minor increases in hunting time. Even though our Baseline Winter Activity scenario was based on bobcat activity of 4 h daily, when hours active are increased to 8, 10, and 12 h, caloric requirements went from 577 kcal to 644, 677, and 711 kcal respectively (Fig. 3). Essentially, tripling time spent active resulted in 124 kcal more required by a bobcat, which could be satisfied by consuming an additional red squirrel or several small rodents per day. In comparison, the cost of increasing time spent hunting even by small increments greatly increased caloric needs; for example, increasing time spent hunting from just 15–30 min results in 137 kcal more required by a bobcat daily. Thus, a bobcat can greatly increase time spent active with little overall energetic impact, but increases in time spent hunting have a disproportionate impact on energy expenditures. We suspect this result reflects the terms used to estimate hunting costs, which were based on an active chase and the need to subdue struggling prey Calder (1984). Unfortunately, we lack a good data set for reparameterizing the hunting costs for bobcats hunting small prey; it would be valuable for further research to refine this estimate.

The high hunting costs estimated in the model might occur when a bobcat engages in a long chase or targets a larger prey animal, such as a snowshoe hare or a deer; we did observe bobcat predation of deer during our study. Still, for the vast majority of hunts, this cost is likely an overestimate. Bobcats can also reduce energetic demands through changes in hunting technique. The congeneric Canada lynx switches strategies when prey density changes; lynx use ambushes increasingly during cyclic hare lows, thus conserving critical energy reserves (O'Donoghue et al., 1998). Individual bobcats are likely to employ ambushes, rather than actively chasing prey, for prey species such as the 1400 g snowshoe hare. Bobcats may quickly abandon the chase should the initial jump after a hare prove unsuccessful (Marston, 1942).

Further, bobcats could adjust to energetic requirements via mass loss. For example, the male bobcat with the large movements weighed 14 kg on 12 December 2009, 12.5 kg on 22 January 2010, and 13 kg on

2 February 2010. Losing mass both provides calories for use to offset expenditures and lowers subsequent movement and thermoregulation costs; we expect mass fluctuations are common in bobcats in winter, as they are for other boreal species (Hodges et al., 2006). No starvation mortality of study animals occurred, nor did we observe any animals that were extremely thin on our study area.

4.1. Bobcat kill rates and ability to acquire sufficient prey

Our winter energetics model estimates the caloric needs for bobcats in a harsh environment, which we then turned into estimates of daily and seasonal needs for prey based on the observed diet of bobcats in this region (Newbury and Hodges, 2018). Although we do not know the hunting success of bobcats in this region, these calculations suggest that bobcats could stay near energy balance with even moderate hunting success. Specifically, this kcal requirement could be satisfied by taking 0.6 snowshoe hares/day but no other prey, a number well in line with the hares consumed by similarly-sized coyotes (0.3–2.3 hares/day) and lynx (0.3–1.2 hares/day) in the Yukon (O'Donoghue et al., 1998). Alternatively, bobcats could stay in energy balance by consuming 1–2 squirrels and 2–3 voles per day, which is roughly proportional to the observed diet (Newbury and Hodges, 2018). This consumption rate would mean a bobcat makes one kill of a small prey animal on average every ~5 h. Such a kill rate is possible. A domestic cat's stomach empties in < 12 h (J.A. King, veterinary technician, personal communication), and there is no reason to suspect a large difference in digestion rates between domestic cats and bobcats.

Dietary studies typically find that bobcat stomachs contain one prey item, typically from a large prey animal, such as deer or lagomorph (Hamilton and Hunter, 1939; Litvaitis et al., 1984; McLean et al., 2005; Newbury and Hodges, 2018). This result makes intuitive sense as large prey would constitute a meal more than satisfying a bobcat's daily caloric requirements. For example, 27 of 79 samples (~34%) examined by Newbury and Hodges (2018) contained a single large prey item such as deer, snowshoe hare, muskrat (*Ondatra zibethicus*), grouse, or bushytailed woodrat, which would easily satisfy bobcat energy requirements under our Baseline Winter Activity scenario (Fig. 4).

Additionally, studies examining the stomach contents of bobcats routinely find multiple prey items (Hamilton and Hunter, 1939; Litvaitis et al., 1984; McLean et al., 2005). For example, 20% (5 of 25) of bobcat stomachs we examined had ≥ 2 prey types, and 3 scat samples contained ≥ 2 prey types (Newbury and Hodges, 2018). These samples were often combinations of a large prey type and a smaller prey type; in fact, one stomach contained deer remains, a snowshoe hare, and a red squirrel (Newbury, 2013). Hamilton and Hunter (1939) observed several bobcat stomachs contained remains of up to 7 small prey animals, including mice and voles, birds. chipmunks, and birds. Bobcats thus appear capable of meeting daily energy requirements through capture of multiple smaller prey animals within short time frames; capturing large prey items such as hares and deer would provide more calories than the estimated daily requirement.

4.2. Costs of thermoregulation and movement

We built our scenarios by assuming bobcats did not require separate thermoregulatory costs. This assumption could be true (a) if their fur provides sufficient insulation such that their T_{lc} is lower than most ambient temperatures they experience, (b) if they behaviorally avoided times and places where ambient temperatures were below T_{lc}, e.g. by resting in snow dens or thick vegetation on extremely cold days, or (c) if they were active on cold days and the waste heat from moving meant they did not need a separate cost for thermoregulation.

Although we do not know the genuine T_{lc}, for this population of bobcats, we strongly suspect it is considerably lower than the − 2.2 °C that Mautz and Pekins (1989) obtained for eastern bobcats. Even if Montana bobcats had a T_{lc} only a few degrees lower than these authors

observed, that would be highly influential on true energetic needs. In our study area, average daily temperatures were below $-2.2\,°C$ for 90 of 90 winter days. However, 79 of 90 winter days had mean temperatures that were above $-10\,°C$. Clearly, knowing the genuine T_{lc} for this population of western bobcats is important given these ambient temperatures.

Behaviorally, we do have evidence that bobcats adjust to ambient conditions.

We observed bobcats reducing movements during extreme cold and snowy periods, seeking shelter from winds, and choosing resting sites that were protected or that enabled basking in sun. For example, in December 2009, the study area experienced an extreme cold spell where daily high temperatures were below $-20\,°C$ for 10 consecutive days; our track surveys showed little to no activity of bobcats. When the cold spell broke, and overnight temperatures were warmer than $-20\,°C$, our track surveys again showed regular bobcat activity. These data suggest bobcats sharply reduced their activity during this cold spell.

Another unknown parameter is how much energy it costs bobcats to travel through deep, uncompacted snow. In New Hampshire, regional occupancy models suggest eastern bobcats prefer areas with low snowcover, but in this region snow-depths varied from 0 to 145 cm and bobcats could in fact spend much of the winter in areas with no or minimal snow cover (Reed et al., 2017). In contrast, the western bobcats in our study area clearly managed to overwinter in deep snow at high elevation and had no snow-free habitat options. Further, snow is hugely variable in its consistency, and other predators (lynx, red fox (*Vulpes vulpes*), coyote, wolverine (*Gulo gulo*), and wolf (*Canis lupus*)) choose habitats and even individual pathways where the snow is more compressed and hence likely to be less energetically costly to travel across or through (Whiteman and Buskirk, 2013; Dowd et al., 2014; Pozzanghera et al., 2016; Droghini and Boutin, 2018). Travel costs are essentially unknown for mesocarnivores travelling through different kinds of snow, although Crête and Larivière (2003) found that the heart-rate of coyote-sized dogs went up only $\sim 5\%$ when travelling through snow compared to travelling on a hard surface. We suspect that in our northern Montana study sites, bobcats were adept at finding routes that minimized exposure to deep fluffy snow. Further, there were numerous freeze-thaw events, wind-scours that created hard crusts, and substantial variation in snow cover in relation to the habitat cover.

4.3. Implications of winter energetics for bobcats in extreme environments

There are several important implications of this energetics model for bobcats. First, based on the results from the Baseline Winter Activity scenario, we conclude that bobcats in this area of Montana may not be seriously out of energetic balance despite the cold temperatures and deep snow that are atypical of the bobcat geographic range. Second, the Baseline Winter Activity scenario deals specifically with average metabolic stresses and dietary requirements of bobcats to remain in daily and overwinter energy balance. However, bobcats face day-to-day variability in individual ability to meet average metabolic needs. This daily variation is affected by prey availability, the bobcat's ability to capture sufficient prey, and abiotic conditions such as extreme cold snaps and snowstorms. It would be rewarding to use more telemetry/satellite locations or accelerometers to obtain fine-scale behavioral detail to link to daily weather.

The energetics model suggest bobcats can maintain energy balance in long winters with deep snows. Although other authors have suggested bobcats are snow-limited, with their northern range limits in fact caused by difficulty in snow and cold (Roberts and Crimmins, 2010), our results suggest otherwise. This result is particularly intriguing because both Canada lynx and coyotes, two mesocarnivores of similar size to bobcats, have geographic ranges that extend throughout northern British Columbia and into the Yukon and Alaska, whereas bobcats have their range limit in central BC (Gooliaff et al., 2018), a limit that

appears to have been stable for the last ~ 80 years (Gooliaff and Hodges, 2018). Lynx specialize on snowshoe hares, but coyotes are generalist predators; it is controversial how much any of these three species compete (Parker et al., 1983; Buskirk et al., 2000a, 2000b; Kolbe et al., 2007, Peers et al., 2013). Our results indicate the bobcats do not have unusually high metabolic needs overwinter, so some other reason must exist for their range limit that is so much further south than that of the two others. Interestingly, bobcats are replaced by ocelots (*Leopardus pardalis*) at the southern margin of their geographic range, and there is a similar area of sympatry between bobcats, coyotes, and ocelots, as there is between bobcats, coyotes, and Canada lynx at the northern margin. We think it would be informative to obtain simultaneous dietary, energetic, and behavioral information for all three species at the actual northwestern edge of the range for bobcats (in central BC), to see if there are differences that can be teased apart to explain this range margin for bobcats. We wonder if there are differences in prey availability that would explain this enigma.

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