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**Costs of locomotion in polar bears: when do the costs outweigh  
the benefits of chasing down terrestrial prey?**

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**Lay Summary:**

Trade-offs between locomotory costs and foraging gains are key to predator-prey interactions.

As climate change forces polar bears to spend more time ashore, their prey base and these trade-offs may be altered. We show that polar bears can profitably capture seasonally available land-based prey like geese over a range of pursuit speeds.

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## **Abstract**

Trade-offs between locomotory costs and foraging gains are key elements in determining constraints on predator-prey interactions. One intriguing example involves polar bears pursuing snow geese on land. As climate change forces polar bears to spend more time ashore, they may need to expend more energy to obtain land-based food. Because polar bears are inefficient at terrestrial locomotion, any extra energy expended to pursue prey could negatively impact survival. However, polar bears have been regularly observed engaging in long pursuits of geese and other land animals and the energetic worth of such behavior has been repeatedly questioned. We use data-driven energetic models to examine how energy expenditures vary across polar bear mass and speed. For the first time, we show that polar bears in the 125 to 235 kg size range can profitably pursue geese, especially at slower speeds. We caution, however, that heat build-up may be the ultimate limiting factor in terrestrial chases, especially for larger bears, and this limit would be more quickly reached with warmer environmental temperatures.

## **Keywords**

locomotion, oxygen consumption, polar bear, predation, snow goose, terrestrial prey, *Ursus maritimus*

## Introduction

The relationship between energetic gain and locomotory cost is a key determinant in predatory behavior and greatly influences predator/prey interactions (e.g. Sinclair et al. 2003; Scharf et al. 2006). In the broadest sense, predatory behavior of mammalian carnivores spans a range from ambushes (e.g. lions (*Panthera leo*) and leopards (*Panthera pardus*)) to rapid, long-distance pursuits (e.g. cheetah (*Acinonyx jubatus*) and spotted hyena (*Crocuta crocuta*) (e.g. Bro-Jørgensen 2013)). A particularly intriguing case involves the interactions of polar bears (*Ursus maritimus*) and lesser snow geese (*Chen caerulescens caerulescens*), a land-based prey that may become an increasingly important seasonal food resource for polar bears as climate changes (Gormezano and Rockwell 2013a,b, 2015).

Polar bears normally use the sea ice as a platform to catch marine prey, particularly ringed seals (*Pusa hispida*), and accumulate a majority of their annual fat reserves from consuming seal pups in spring (e.g. Stirling and Øritsland 1995). In more southern polar bear populations, it is thought that this energy store helps sustain the bears during the ice-free period each summer (e.g. Stirling and Derocher 1993; Regehr et al. 2007). With warmer temperatures leading to earlier sea ice breakup, access to this energy-rich spring seal diet may become limited, potentially forcing the bears to expend energy seeking land-based food to compensate for energy deficits (e.g. Stirling and Derocher 2012; Gormezano and Rockwell 2013a, 2015; Lunn et al 2016). Any increased effort to obtain food is of concern because polar bears are considered inefficient at walking (Øritsland et al. 1976; Best 1982; Hurst et al. 1982a; Hurst et al. 1982b), exhibiting higher rates of oxygen consumption with increased walking speed than predicted for mammals of their size (Taylor et al. 1970; Fedak and Seeherman 1979). The higher rates of energy use have been attributed to their morphology, particularly their large, heavy limbs (Øritsland et al.

1976; Hurst 1982a; Hurst et al. 1982b), a characteristic shared by male lions that similarly have relatively high costs of locomotion (Chassin et al. 1976). Despite these energetic limitations, polar bears are known to walk long distances in search of prey on sea ice and land (e.g. Born et al. 1997; Amstrup et al. 2000; Parks et al. 2006; Anderson et al. 2008; Rockwell et al. 2011) but generally use more energy-conserving stalking or “still-hunting” techniques to capture seals and other marine mammals on the sea ice (e.g. Stirling 1974; Smith 1980).

Some polar bears, especially those forced ashore when the sea ice melts in summer, have been observed running on land in pursuit of terrestrial prey (e.g. Brook and Richardson 2002; Iles et al. 2013 and references therein). Given their locomotive inefficiency and potential to overheat in warm weather (Best 1982; Øritsland 1970; Øritsland and Lavigne 1976), it is unclear whether these more intensive pursuits can be energetically profitable (Lunn and Stirling 1985; Iles et al. 2013). In the only examination of this issue thus far, Lunn and Stirling (1985) used a calculation based on Hurst et al. (1982a) to suggest that a 320 kg polar bear chasing a goose at 20 km/h for more than 12 seconds would spend more energy in the pursuit than could be obtained from consuming it. Despite the speed and mass specificity of that projection, many authors have used this threshold in evaluating observations of polar bears chasing various land-based prey (e.g. caribou, *Rangifer tarandus* (Brook and Richardson 2002); Barnacle geese, *Branta leucopsis* (Stempniewicz 2006); Thick-billed Murres, *Uria lomvia* (Donaldson et al. 1995); lesser snow geese (Iles et al. 2013)) and questioned the energetic worth of the observed predatory behaviors.

The exact energetic costs associated with land-based hunting behavior are especially important for polar bears in western Hudson Bay where recent warming trends are rapidly diminishing ice extent and duration (Gagnon and Gough 2005; Stirling and Parkinson 2006; Lunn et al 2016). If polar bears come ashore with nutritional deficits (e.g. Stirling and Parkinson

2006; Regehr et al. 2007), any calories obtained on land may become increasingly important for survival (Gormezano and Rockwell 2013a,b, 2014, 2015) unless the net energetic gain from foods obtained on land exceeds the energetic costs required to obtain them. In western Hudson Bay, snow geese comprise an increasing proportion of polar bears' land-based diet due in part to both increased temporal overlap of the two species and to greatly increased abundance of snow geese (Gormezano and Rockwell 2013a, 2015). Given that polar bears in this region spend increasingly more time on land and thus have more opportunities for terrestrial foraging, we constructed predictive models that for the first time estimate the metabolic costs of terrestrial locomotion for polar bears of multiple sizes traveling at various speeds. We then use the best-fit model to evaluate when a polar bear would profit from chasing and catching molting snow geese, a common terrestrial prey species during summer.

In the following, we revisit the only published data on the metabolic costs of locomotion across a range of speeds for polar bears of multiple sizes. We assess the profitability of pursuing flightless geese using data-driven energetic models that simultaneously account for the effects of polar bear speed and mass. We show that pursuits lasting longer than 20 minutes in duration can be energetically profitable, though this depends importantly on the speed and mass of polar bears, and that successful pursuits of even distant geese can result in net energetic gains for some polar bears. Further, we show that the smaller sized and younger bears that could take more advantage of this profitability include those whose survival in western Hudson Bay is lower (Lunn et al. 2016) and that may be more impacted by climate change (Regehr et al. 2007).

## Methods

To develop a data-driven model that allows oxygen consumption (and thus metabolism) to scale with polar bear speed and mass, we extracted original data from the three published studies that reported measurements of  $O_2$  consumption ( $\text{ml } O_2 \text{ g}^{-1} \text{ h}^{-1}$ ) as a function of walking speed for polar bears that weighed 125, 155, 190 and 235 kg. The 125 and 155 kg animals were subadult males (as defined by Watts et al. 1991), the 190 kg animal was a 4 year old female (Hurst et al. 1982a) and the 235 kg animal was an approximately 4 year old male (Øritsland et al. 1976). We used the means of the multiple trials of each bear at each speed as the best estimates of  $O_2$  consumption for each mass and speed. Both linear (Hurst et al. 1982a; Øritsland 1970) and double exponential (Hurst et al. 1982a) regression models have previously been used to describe how oxygen consumption changes with speed for different-sized bears. Here, we first considered three potential models to describe the general shape of the relationship between polar bear speed ( $S$ ) (we use this term rather than velocity ( $V$ ) as used by Hurst et al. (1982a)) and oxygen consumption ( $VO_2$ ) using data from Øritsland et al. (1976), Hurst et al. (1982a), and Watts et al. (1991). Our initial model set included:

1) a linear model that allows metabolism to increase at a constant rate with increasing speed,

$$VO_2 = P + bS, \quad [1]$$

2) an exponential model that allows metabolism to accelerate with increasing speed,

$$VO_2 = Pe^{bS}, \quad [2]$$

and 3) a double-exponential model that allows metabolism to more flexibly scale with speed,

$$VO_2 = Pe^{bS^c}, \quad [3]$$

where  $P$  is polar bear postural cost (*i.e.* the energetic cost of maintaining an upright posture when speed is zero),  $e$  is the natural log (2.718...), and  $b$  and  $c$  are exponents that describe the rates at which oxygen consumption changes with movement speed ( $S$ ). From previous work (Hurst et al. 1982b), postural costs are known to depend on mass. Thus, in all models we fixed the postural costs at the expected values for each polar bear mass based on the equation in Hurst et al. (1982b) following Taylor et al. (1970):

$$P = 1.056 \cdot \text{mass}^{-0.25} \quad [4]$$

By fixing the postural costs (the Y-intercept) based on this equation rather than allowing the postural costs to be estimated based on model fit, we improve the biological realism of our models outside the range of our data (*i.e.*, when speed is 0), while only slightly sacrificing goodness-of-fit within the range of our data (speeds of 1.8 - 7.92 km/h). We note, however, that results were qualitatively similar whether postural costs were fixed based on equation 4 or estimated based on our data. We evaluated relative support for the models using Akaike's Information Criterion (AICc; Akaike 1973) and found that the exponential and double-exponential models received similar support (Table 1;  $\Delta\text{AICc} = 0$  and 0.5, respectively), and greatly outperformed the linear model ( $\Delta\text{AICc} = 24$ ).

We then constructed several additional models to evaluate potential effects of polar bear mass on oxygen consumption, beyond the effects on postural cost in equation 4. Because the exponential and double-exponential models received similar support and produced similar predictions across the range of our data, we constructed a suite of models that allowed mass to influence  $b$  and/or  $c$  in equations 2 and 3 (Table 1). We used AICc and Akaike weights to evaluate relative support among different parameterizations and assess the relative effects of mass and speed on oxygen consumption.

Using model projections of oxygen consumption based on our top model, and following Lunn and Stirling (1985), we calculated the time threshold (hereafter “inefficiency threshold”) beyond which the calories expended to chase a goose exceeded the calories obtained from consuming it for polar bears ranging in mass from 125 kg to 235 kg and over a range of speeds from 0 to 7.9 km/h. For comparative purposes with previous work (Lunn and Stirling 1985) and because polar bears are known to run at speeds up to 29 km/h (Harrington 1965), we also projected inefficiency thresholds to 20 km/h. We discuss the assumptions and limitations of those extrapolations in the Discussion.

Estimating the usable energy available to a polar bear eating a goose requires knowing (a) the energy in the part(s) of a goose that are eaten, and (b) the digestibility of the energy in the parts of the goose eaten. Polar bears that successfully capture and eat a variety of prey including seals (Smith 1980, Best 1985) and geese (Iles et al. 2013, Gormezano and Rockwell 2015, pers observations) rarely consume the less digestible portions including hair and feathers and usually avoid eating the gastrointestinal tract and the entire skeleton. Thus, we assumed that polar bears primarily consumed the breast, leg muscle, gizzard and fat stores from a captured goose. We estimated the caloric value of these eaten parts of the goose using adult female goose body composition data from Ankney and MacInnes (1978) (as did Lunn and Stirling 1985) during the post-hatch period when many instances of predation have been observed (Iles et al. 2013). At this post-hatch time, adult female geese ( $n = 35$ ) had negligible amounts of fat and  $163.3 \pm 4.0$  of protein within the gizzard, breast and leg muscles (Table 3 in Ankney and MacInnes 1978) which would provide 702.5 kcal assuming an energy to protein conversion of 4.3 kcal/g protein (Robbins 1993). However, polar bears cannot be expected to digest all the available protein so some discount is necessary.



Grizzly and Black Bears digested 89-96% of crude protein in the meat from various mammals and birds (Pritchard and Robbins 1990) whereas digestibility of crude protein for bears fed whole birds or mammals was less (85.5 +/- 2.2%) because of the non- or less-digestible parts (e.g., feathers, hair, skeleton)(Pritchard and Robbins 1990, Robbins 1993). Similarly, captive polar bears fed various parts of ringed seals (*Phoca hispida*) digested 72-95% of protein nitrogen with the highest digestibility occurring when polar bears ate seal muscle and viscera and the lowest digestibility when the skeleton, skin, and blubber were also eaten (Best 1985). We assumed that polar bears digested 95% of protein when eating only the gizzard, leg and breast muscle of the goose; digestibility of protein would be much lower (72-85%) if polar bears also ingested other less digestible parts of the whole goose. We present results for the most likely scenario where polar bears ate the gizzard, leg and breast muscle of the goose and thus gained 667.4 kcal per goose (702.5 total kcal of which 95% was digested).

Finally, to determine the conditions under which inefficiency thresholds would be reached during pursuits of flightless geese, we calculated the duration of pursuits resulting from different combinations of polar bear speeds and initial distances from geese. We assumed geese fled from pursuing bears at 2 m/s; a value slightly higher (and thus more conservative in terms of polar bear profitability analysis) than the reported maximum sustained running speeds of 0.8 – 1.2 m/s, considered ‘moderate’ to ‘fast’ for similar sized geese (Codd et al. 2005; Hawkes et al. 2014). We calculated the time required for a polar bear to capture a goose as:

$$T = \frac{D}{S_{\text{bear}} - S_{\text{goose}}}, \quad [5]$$

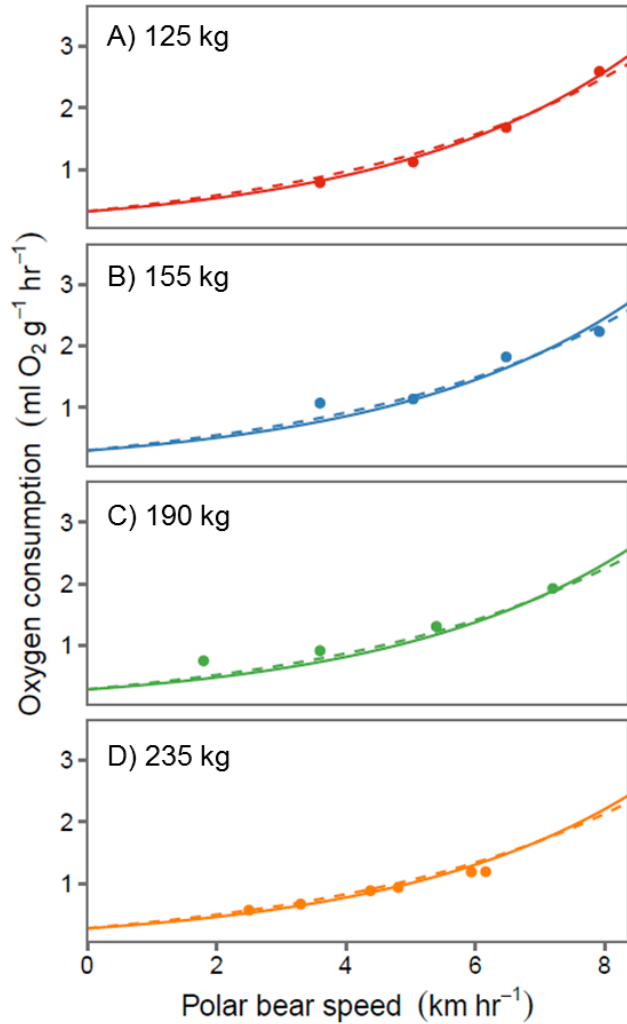
where D is the initial distance between the bear and the goose and  $S_{\text{bear}}$  and  $S_{\text{goose}}$  are their respective speeds. For each combination of bear mass, speed, and initial distance, we calculated

the inefficiency threshold and compared this to the chase duration to determine if the pursuit resulted in a net surplus of energy to the bear.

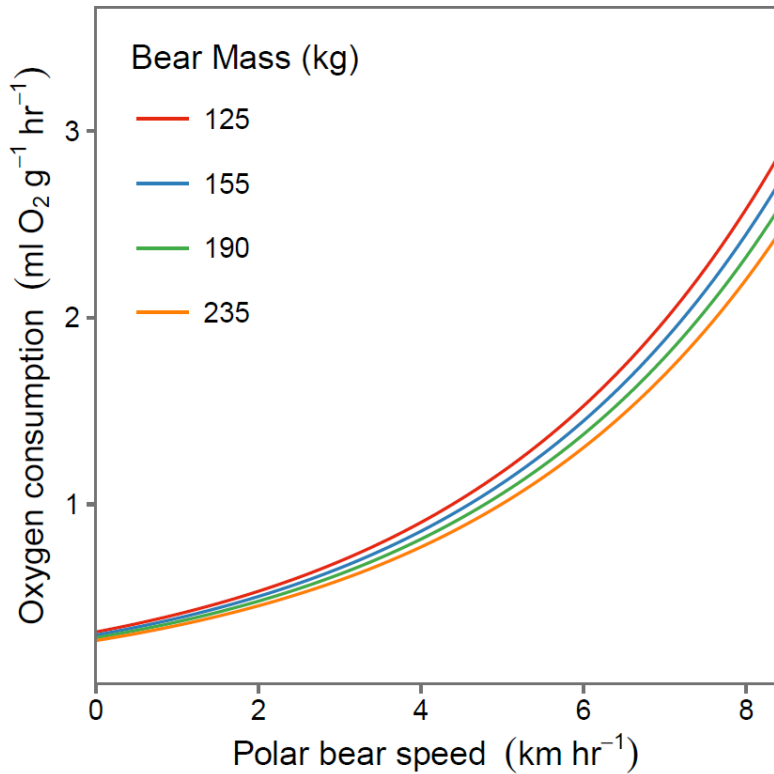
All analyses were performed using the R statistical programming language (version 3.2.3; R Development Core Team 2008).

## Results

The relationship between polar bear movement speed and oxygen consumption was best described by either an exponential or double-exponential model, indicating that metabolism increases exponentially at higher speeds (Figure 1). We found no support for an effect of polar bear mass on the exponents in either model (Table 1). Since postural cost depends on polar bear mass (equation 4) but the shape of the exponential relationship between polar bear speed and oxygen consumption does not, larger bears are more efficient than smaller bears on a proportional basis across all movement speeds (Figure 2). Because the exponential model received slightly higher support and was more parsimonious (i.e., used fewer parameters) than the double-exponential model, we used the exponential model to generate estimates of oxygen consumption as a function of polar bear mass and speed (Figure 2), and subsequently, to determine energetic inefficiency thresholds and profitability while chasing flightless geese. We note, however, that the double-exponential model produced very similar predictions as the top model across the range of data (Figure 1, compare solid and dashed lines).

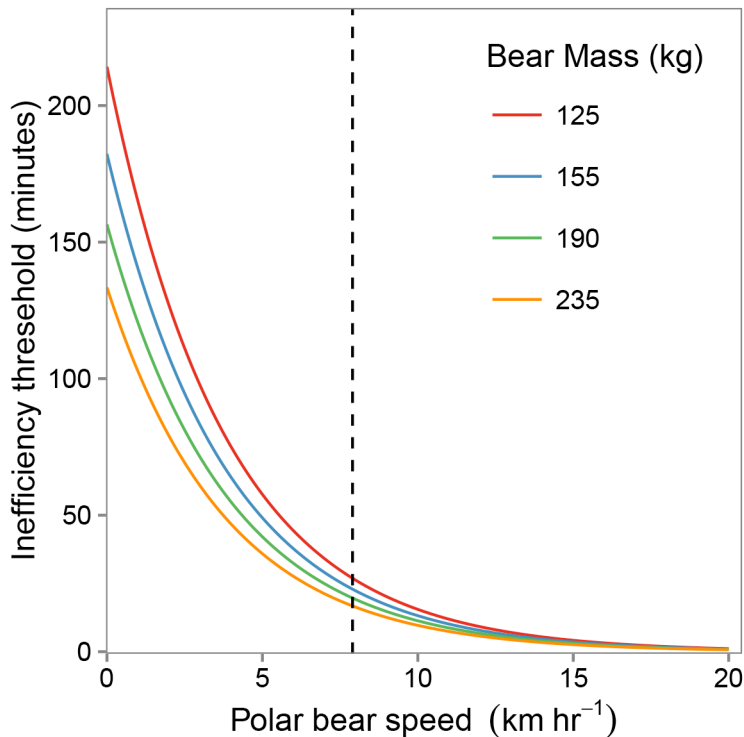


**Figure 1.** Mass-specific oxygen consumption increases with movement speed. Postural costs (Y-intercept) are affected by polar bear mass according to equation 4. The top model based on AICc was a single-exponential model (solid lines). A double-exponential model received similar support ( $\Delta\text{AICc} = 0.5$ ) and made similar predictions across the range of data (dashed line).



**Figure 2.** Mass-specific oxygen consumption increases with movement speed. Postural costs (Y-intercept) are affected by polar bear mass according to equation 4. Larger bears are proportionately more efficient than smaller bears. Curves are based on predictions from top model (exponential model; equation 2) which when parameterized is  $VO_2=(1.056*\text{mass}^{-0.25})*e^{0.2626*S}$ .

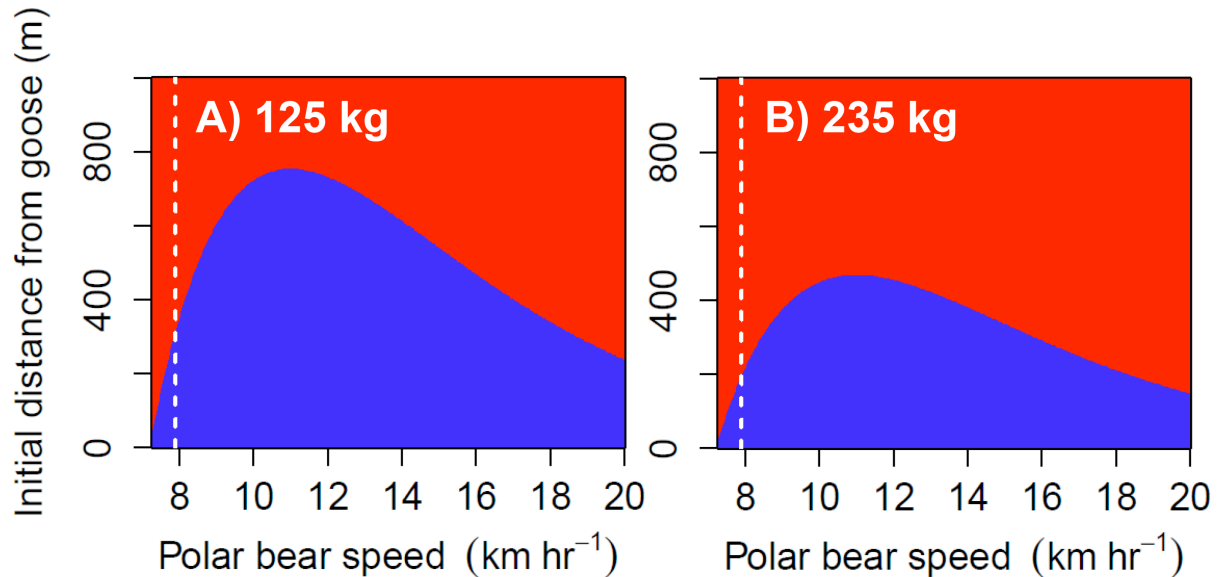
Combining results from our oxygen consumption models with the energetic value of a female lesser snow goose, we calculated that a 125 kg polar bear could chase a goose for 26.9 minutes at 7.9 km/h (the maximum speed of polar bears for which oxygen consumption measurements were recorded) before it becomes energetically unprofitable. By contrast, the inefficiency threshold for a 235 kg bear at 7.9 km/h was 16.7 minutes. Because energy consumption increases with speed, the inefficiency threshold decreases with increasing speed for bears of any mass. Despite larger bears having lower proportional oxygen consumption than smaller bears (Figure 2), the higher absolute mass of larger bears results in lower inefficiency thresholds across the range of speeds for which there are data (Figure 3). Because of this, smaller bears can sustain chases that are longer in duration.



**Figure 3.** Time "inefficiency" threshold beyond which calories expended by a polar bear to chase an adult female goose exceeds the calories obtained from consuming it, as a function of speed of the chase and polar bear mass. Note that projections for speeds greater than 7.9 km/h (dashed line) are extrapolations beyond the available data and should be interpreted with caution, but are pictured for comparison with extrapolations by previous studies. The Inefficiency Threshold is calculated as:  $I = 667.4 / (VO_2 \cdot \text{mass} \cdot 4.735) / 60$  where 667.4 is the caloric value of a goose, mass-specific  $VO_2$  is estimated as in the legend of Figure 2 and 4.735 is the standard conversion of 1L of oxygen to kilocalories.

Ultimately, the time required to capture terrestrial prey depends on the initial distance between the polar bear and prey and the relative speeds of the bear and the prey. If the chase duration exceeds the energy inefficiency threshold for that particular pursuit speed, polar bears will lose energy even from pursuits in which they successfully capture geese. We found that polar bears were capable of capturing geese before reaching their inefficiency threshold for a wide range of pursuit scenarios (Figure 4, blue areas). Smaller bears (*i.e.* 125 kg) were capable

of gaining energy from pursuits of geese up to 754 m away, while larger bears (*i.e.* 235 kg) could gain energy from pursuits of geese up to 468 m away.



**Figure 4.** Profitability of capturing flightless snow geese for 125 kg (A) and 235 kg (B) polar bears. Initial distance from flightless geese and polar bear speed influence the time required to capture a goose, while polar bear mass and speed influence the inefficiency threshold (chase duration beyond which energy expenditures exceed energy gains from consuming a 667.4 kcal goose). Chases that are shorter in duration than the inefficiency threshold are colored in blue (resulting in a net energy surplus for polar bears). Note that because geese are capable of running at 2 m/s (or 7.2 km/h), bears are incapable of capturing geese when moving slower than this speed. Areas to the right of the white dashed line are extrapolations outside the range of data, but are pictured for comparison with extrapolations in previous studies.

## Discussion

The best supported predictive model for estimating the metabolic costs of terrestrial locomotion for polar bears of different sizes was a simple exponential model (Figure 2). Importantly, the shape of the exponential relationship between polar bear speed and metabolic cost did not depend on polar bear mass, only the postural costs (y-intercept) were mass-dependent; the implication being that smaller bears therefore spend proportionately more energy

for locomotion than larger bears (Figure 3). Previous studies have shown that postural costs (energy costs when speed is zero) are greater for smaller bears (Scholander et al. 1950; Hurst et al. 1982b), a pattern observed in smaller and immature animals in general (Taylor et al. 1970; Lavigne et al. 1986). These higher postural costs with decreasing polar bear mass combined with similar exponential increases in the energy costs of locomotion with travel speed regardless of mass result in smaller bears having proportionately higher locomotion costs than larger bears at a given travel speed.

Earlier studies have suggested that the higher locomotive costs of smaller bears could be related to increased stride frequency, as more steps will be needed to maintain the same speed as larger bears (Heglund and Taylor 1988; Best et al. 1981). Energy cost per gram of body weight per stride is relatively constant across animals of drastically different masses moving at the same speed (Heglund et al. 1982), so although heavier animals require more energy to move per stride, the longer stride length and lower stride frequency could result in increased efficiency over the same distance (Heglund et al. 1982). Incremental rates of energy use during terrestrial locomotion can also change with transitions to different gaits (Chassin et al. 1976; Heglund and Taylor 1988; Reilly et al. 2007; Watson et al. 2011), although this has not yet been studied in polar bears and warrants further attention because it could affect the shape of oxygen consumption curves at higher speeds.

Pursuits (and capture) of flightless snow geese lasting longer than 12 seconds have been documented (Iles et al. 2013) and we have observed multiple examples of this behavior in recent years (our unpublished data). Our analyses here indicate that these observations are actually to be expected, given that prolonged (i.e. over 20 minutes) pursuits of even distant geese (i.e. farther than 500m) can be energetically profitable, especially for polar bears in the size range for

which there are data (Figures 3 and 4). Of those, smaller bears are capable of profitably engaging in pursuits of more distant geese, and at higher pursuit speeds, given their lower overall level of energy expenditure (Figure 4). In western Hudson Bay, sub-adult polar bears (those that are included in the studied size range) as well as females with cubs tend to arrive onshore in spring earlier than larger mature individuals (Rockwell and Gormezano 2009). Interestingly, our results suggest that these younger and smaller bears, that have recently been shown to have lower survival (Lunn et al 2016) and that may be disproportionately affected by lost opportunities to hunt seals due to climate change (Regher et al 2007; Rockwell and Gormezano 2009), should have an inherently better ability to recover caloric deficits via terrestrial prey.

Prolonged chases of flightless snow geese can be energetically profitable over a range of pursuit speeds for polar bears in the 125-235 kg size range. The same is likely true for larger bears, those outside the range of available oxygen consumption data, since only postural cost (Y-intercept) is mass dependent and it scales at the 0.25 power (Figure 4; Taylor et al 1970). Extrapolations past the upper limit of speeds for which there are data assume that the functional basis for the modeled trend remains the same, an assumption that may be violated if polar bears change gait and energy efficiency at higher speeds. Nevertheless, based on our top model, we project that a 320 kg bear running at 20 km/h would expend the calories contained in an adult goose in 33 seconds, a value that is reasonably comparable to the estimate of 12 seconds previously suggested by Lunn and Stirling (1985) using a different model. However, we note that our model also predicts that 320 kg bears can more profitably engage in much longer pursuits at slower speeds (e.g. our model predicts that pursuits of geese lasting up to 13.3 minutes are energetically profitable for a 320 kg polar bear running at 7.9 km/h).



Although polar bear locomotion is considered relatively inefficient, they typically walk slowly with a steady gait of about 5.5 km/h (Stirling 1988). They average 1 to 5 km/h over longer distances, periodically interspersed with rest stops, and can sustain these speeds for extended periods while covering large distances (Harrington 1965; Amstrup et al. 2000; Anderson et al. 2008; Durner et al. 2011; Whiteman et al. 2015). For example, Amstrup et al. (2000) reported many polar bears sustaining average travel on the ice at >4 km/h for up to 20 hours, with some maintaining these speeds for >40 hours. In a controlled experiment, polar bears trained to walk on treadmills were similarly able to walk for long periods, continuing exercise for up to 90% of 6 hour walking sessions (Best 1982). However, during these trials polar bears behaviorally thermo-regulated by leaving the treadmill temporarily to ingest snow when their core temperatures reached a particular threshold (Best 1982). Best (1982) suggested that hyperthermia, not fatigue, was more likely a limiting factor to continuous locomotion. Polar bears have also been observed sustaining higher speeds (approaching 10 km/h) for shorter periods of time while on the ice (i.e., 1-8 hours) (Amstrup et al. 2000) where low ambient temperatures and strong winds would likely reduce the risk of hyperthermia (Best 1982).

By contrast, while on land during the ice-free season in western Hudson Bay when ambient temperatures are considerably higher, polar bears limit their daily movements, remaining inactive for long periods (Knudson 1978; Latour 1981). However, they have been observed engaging in faster-paced pursuits after caribou and waterfowl (e.g. Brook and Richardson 2002; Iles et al. 2013; our unpublished data). In such cases, hyperthermia, rather than lack of profitability, may be a limiting factor to sustained activity for several reasons. Polar bears are typical of non-sprinting mammals in that almost all the heat produced during exercise is immediately dissipated and little is stored (Taylor et al. 1970; Best 1982) making warmer

ambient temperature conditions particularly problematic since it reduces the potential for heat dissipation while exercising. For example, 218-239 kg polar bears walking at 7.9 km/h reached their upper critical temperature (when core body temperature can no longer be regulated) at about -33 C. Further, these captive bears could only sustain this activity at temperatures up to -20 C when allowed to ingest snow before returning to walk (Best 1982).

Interestingly, many pursuits by wild bears have been observed in or near ponds, lakes and rivers (Iles et al. 2013; our unpublished data) with the bear often lying in shallow streams and ponds immediately after the pursuit (Figure 5). Immersion in water has been shown to substantially reduce a polar bears' core body temperature both before and after sustained exercise (Øritsland 1969; Frisch et al. 1974). In general, the thermoregulatory costs of exercise for polar bears can be somewhat dissipated by certain behaviors but these costs likely often constrain the duration and speed of a wild goose chase especially during warm summer days.

Additional research is clearly needed to fully understand thresholds of inefficiency of foraging pursuits associated with polar bear locomotion. This is especially true for larger-sized bears and for all bears traveling near their maximum speeds. Such data are crucial for understanding the potential importance of land-based foraging behavior. Polar bears currently consume various foods on land (e.g. Gormezano and Rockwell 2013a,b and references therein) but the profitability of these foods and their contribution towards the persistence of polar bears in the face of climate change remains debatable (e.g. Gormezano and Rockwell 2015; Rode et al 2015; Pilfold et al 2016). To clarify these issues, studies are required that either provide complete data allowing the calculation of energetic and nutritional costs and gains or (preferably) that allow those costs and gains to be directly measured.



Figure 5. A sub-adult male polar bear in the Mast River (Wapusk National Park) after killing at least 5 flightless snow geese in 3 chases. After the chases the bear walked into the river, laid down and drank periodically. Photographed on 13 July 2013 by RF Rockwell.

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**Table 1.** Model selection results incorporating effects of mass on the relationship between speed and oxygen consumption. Model parameters are: postural costs ( $P$ ), polar bear movement speed ( $S$ ), polar bear mass in kg ( $mass$ ), single and double exponents ( $b$  and  $c$ , respectively), and scaling parameters ( $m1$  and  $m2$ ) that relate the single exponent and the double exponent to polar bear mass. In all models, postural costs are described by equation 4 and thus depend on polar bear mass.

Model	logLik	AICc	$\Delta$ LogLik	$\Delta$ AICc	par	weight
$Pe^{bS}$	10.1	-15.5	12	0	2	0.288
$Pe^{bS^c}$	11.3	-15	13.2	0.5	3	0.223
$Pe^{(b+m1*mass)S^{(c+m2*mass)}}$	14.9	-14.7	16.7	0.7	5	0.199
$Pe^{bS^{(c+m2*mass)}}$	12.3	-13.6	14.2	1.9	4	0.113
$Pe^{(b+m1*mass)S^c}$	12.2	-13.4	14.1	2.1	4	0.101
$Pe^{(b+m1*mass)S}$	10.3	-12.8	12.1	2.7	3	0.076
$P + bS$	-1.8	8.5	0	24	2	<0.001