ECOPHYSIOLOGY

High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear

A. M. Pagano,[1,2]* G. M. Durner,[1] K. D. Rode,[1] T. C. Atwood,[1] S. N. Atkinson,[3] E. Peacock,[1] D. P. Costa,[2] M. A. Owen,[4] T. M. Williams[2]

Regional declines in polar bear (*Ursus maritimus*) populations have been attributed to changing sea ice conditions, but with limited information on the causative mechanisms. By simultaneously measuring field metabolic rates, daily activity patterns, body condition, and foraging success of polar bears moving on the spring sea ice, we found that high metabolic rates (1.6 times greater than previously assumed) coupled with low intake of fat-rich marine mammal prey resulted in an energy deficit for more than half of the bears examined. Activity and movement on the sea ice strongly influenced metabolic demands. Consequently, increases in mobility resulting from ongoing and forecasted declines in and fragmentation of sea ice are likely to increase energy demands and may be an important factor explaining observed declines in body condition and survival.

As the most carnivorous and only marine-living ursid, polar bears are lone among bears in their reliance on marine mammal prey. Evolution of this Arctic apex predator included behavioral and physiological adaptations that distinguish polar bears from terrestrial bears (*1*), which has made them dependent on the sea ice and may increase their vulnerability to climate change (*2*). As a consequence of living in this labile marine habitat, polar bears occupy expansive home ranges that are considerably larger than those occupied by other ursids (*3*) or predicted for similarly sized terrestrial carnivores (*4*). They also exhibit remarkable abilities to swim for extended distances (*5*). However, such long-distance movements, whether walking or swimming, necessitate substantial energetic resources to satisfy locomotor demands (*6*, *7*). Historically, sufficient resources were afforded through the availability of fatty, energy-dense seal prey, which could be hunted efficiently from the sea ice (*8*). Presently, the sea ice minimum extent across the Arctic is decreasing at a rate of 14% per decade, spring break-up is occurring earlier, and fall freeze-up is occurring later (*9*). This decline in sea ice is likely reducing access to, and abundance of, seal prey (*10*).

Because metabolism determines the rate at which organisms require energy from their environment (*11*), measures of polar bear metabolic rates provide an important metric for linking declines in Arctic sea ice to polar bear survival. Changes in energy balance resulting from increased energy expenditure or reductions in foraging opportunities could lead to declines in body condition, survival, and reproductive success. Previous studies have reported that walking costs for polar bears are greater than predicted for other similarly sized mammals (*6*, *12*). Yet, models predicting polar bear annual field metabolic rates (FMRs) assumed that FMRs would be relatively low because of the bear's sit-and-wait style of hunting and theorized ability to reduce metabolism while fasting (*13*, *14*), similar to that of denning bears (*13*, *15*). However, measures of mass loss and body temperature suggest that metabolic rates of fasting polar bears during the summer are in fact greater than those of denning bears (*16*–*18*). Despite this improved understanding of fasting metabolism, no study has provided quantitative estimates of the FMRs of active polar bears on the sea ice where they spend most—and in many areas of their range, all—of the year.

We measured the FMRs of female polar bears (*n* = 9) during April 2014–2016 in the Beaufort Sea (Fig. 1A) over 8 to 11 days each year using doubly labeled water (DLW) (supplementary materials) (*19*). On the same animals, we deployed global positioning system (GPS)–equipped video camera collars and archival loggers with tri-axial accelerometers and conductivity sensors to determine activity and behavior in order to assess the causes of variation in FMRs (Fig. 1) (*19*). We determined individual energetic balance using video-derived observations of foraging and measures of blood biochemistry, body mass, and body composition. Additionally, we measured the resting metabolic rate (RMR) of a captive adult female polar bear using open-flow respirometry to assess baseline energetic costs of the species relative to free-ranging polar bears and other mammals.

Like other members of the order Carnivora whose diet is exclusively meat (*20*), polar bears exhibit greater RMRs as compared with predictions for other terrestrial mammals (derived from omnivores, carnivores, and foliovores; RMR = 70 × mass$^{0.75}$) (Fig. 2) (*21*). RMRs measured from a single captive polar bear over six sessions averaged 0.34 ml O$_2$ g^{-1} h^{-1} (SE = 0.01) with a low, post-absorptive (fasting) value of 0.30 ml O$_2$ g^{-1} h^{-1}, which converts to 37.1 MJ day^{-1}. On a mass-specific basis, this post-absorptive RMR was within 0.5 to 11.4% of post-absorptive RMRs previously reported for subadult polar bears (*22*, *23*), which is 17% greater than measurements from polar bears while denning (*24*) and 2 to 21% greater than other ursids while resting or denning (Fig. 2) (*19*). Thus, carnivory and large body mass set a comparatively high maintenance cost for polar bears that must be satisfied to remain in energetic balance.

As a result, the FMR of polar bears is high relative to predictions for terrestrial mammals generally (*25*) and consistent with expected levels derived solely from other mammalian carnivores (*26*). Our measured FMRs averaged 1.6 times previously assumed values for polar bears (SE = 0.1, range = 1.0 to 2.6) (*13*, *14*). Daily FMRs measured over 8 to 11 days, averaged 0.45 ml CO$_2$ g^{-1} h^{-1} (SE = 0.04, *n* = 9 bears), which converts to 51.6 MJ day^{-1} (SE = 6.2, *n* = 9 bears) or 12,324.7 kcal day^{-1}. These values ranged from 0.6 to 1.1 times predicted FMRs [mean ($\bar{x}$) = 0.8, SE = 0.1] for similarly sized marine and terrestrial mammalian carnivores (*26*) and 2.5 to 5.2 times predicted RMRs based on body mass ($\bar{x}$ = 2.8, SE = 0.3) (Fig. 3A and table S1) (*21*). Daily FMR was 1.5 to 2.8 times the post-absorptive RMR ($\bar{x}$ = 2.0, SE = 0.2) measured in this study. On average, daily FMR was 2.6 times (*17*) and 4 times (*27*) predicted values for male polar bears fasting on land.

To remain in energy balance with these elevated metabolic demands, polar bears have evolved hunting tactics to prey on high energy-content prey, such as ringed seals (*Pusa hispida*), and preferentially feed on their energy-dense blubber (*13*). Using our measures of daily FMR, we estimated that a solitary female bear on the spring sea ice would on average need to eat either one adult ringed seal, three subadult ringed seals, or 19 newborn ringed seal pups every 10 to 12 days to remain in energetic balance (Fig. 4A). Our estimates corroborate observations that bears in the early summer typically kill an adult or subadult ringed seal every 5 days (*8*). However, this rate of consumption would be necessary simply to energetically break even. Polar bears put on the majority of their body fat in the late spring and early summer (*13*) and can reach a relative fatness of 1 kg fat per kg lean body mass (*28*). To obtain this body condition, bears would either need to reduce their energy demands or increase their rate of food consumption.

Using video collar data, we documented bears' hunting behavior and foraging success. Bears used sit-and-wait tactics to hunt seals 90% of the time, and stalking comprised the remaining 10% of hunts (movies S1 to S4) (*19*). Bears

[1]U.S. Geological Survey, Alaska Science Center, Anchorage, AK 99508, USA. [2]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA 95060, USA. [3]Post Office Box 19, Group 7, RR2, Dugald, Manitoba R0E 0K0, Canada. [4]Institute for Conservation Research, San Diego Zoo Global, San Diego, CA 92027, USA.
*Corresponding author. Email: apagano@usgs.gov

that successfully killed and ate adult or sub-adult ringed seals either gained or maintained body mass, whereas bears that only scavenged or showed no evidence of eating lost mass (Fig. 4, B, C, and D). Land-based remains of subsistence-harvested bowhead whale carcasses (*Balaena mysticetus*) provided an alternative food resource for two bears (Fig. 4, B and D), although 91% of their telemetry data were on the sea ice and away from this resource. Scavenging the muscle from previously killed seals was also common (Fig. 4D) and consistent with previous observations of polar bear foraging on the sea ice (8, 13).

Four bears lost ≥10% of their body mass over the 8- to 11-day period (Fig. 4B and table S1), with an average loss of 1% per day (1.95 kg day^{-1}). This is 4 times the percent mass lost per day and 2.2 times the kilograms lost per day documented in fasting polar bears on land (16), which typically exhibit lower activity levels than those of the bears in this study (18). Nevertheless, this change in body mass is within the range of the percent mass loss observed in other carnivores (29, 30). Of these four bears, one lost a greater amount of lean body mass than fat mass (Fig. 4B and table S1), which suggests that she was in a prolonged fasting condition (16). This was confirmed with changes in serum urea/creatinine (U/C) ratios (an indicator of fasting for >7 days) (table S1) (19, 31). Additionally, changes in U/C ratios over the 8- to 11-day period were strongly positively correlated with changes in body mass [coefficient of determination (R^2) = 0.62, P = 0.01, n = 9 bears].

Despite the use of efficient sit-and-wait hunting tactics, polar bears in the spring exhibited activity patterns typical of other large terrestrial carnivores (19). Activity rates (the percentage of time engaged in nonresting behaviors) derived from accelerometers, which were recorded continuously throughout each day, ranged from 22 to 40% ($\bar{x}$ = 34%, SE = 2.8, n = 6 bears) (fig. S2C). Bears spent 28% of the time walking (SE = 2.3, n = 6 bears) and only 0.3% of the time swimming (SE = 0.15, n = 6 bears) (fig. S2C). Activity rates derived from video collars (which recorded only during daylight hours) ranged from 13 to 60% of the day ($\bar{x}$ = 32%, SE = 5.1, n = 9 bears) (fig. S2D). These activity rates are similar to those observed for adult and subadult polar bears on the summer sea ice (34.6% of the time active) (8) but are greater than observations from a breeding adult female polar bear on the spring sea ice (26.7% active) (32). Breeding females are known to exhibit reduced activity and devote less time to hunting as compared with that of nonbreeding individuals (32). In the present study, seven of the nine bears interacted with at least one adult male. However, the activity levels we observed were greater than measures derived from activity sensors on adult female polar bears on the sea ice of the Beaufort Sea during April (25% active) (18) and solitary female polar bears on the sea ice in April (16.9% active) in the Canadian Arctic (33), indicating marked variability in the ac-

tivity levels of this species depending on seasonal, geographical, and reproductive factors. The activity levels for polar bears were less than the activity levels documented in other bear species ($\bar{x}$ = 54% active) (34) but were similar to activity levels reported for other large terrestrial carnivores ($\bar{x}$ = 39% active) (supplementary materials) (19).

Ultimately, the ability of polar bears to achieve energy balance is dictated by the acquisition of metabolizable energy versus expenditure from basal metabolism, specific dynamic action, thermoregulation, reproduction, growth, and locomotion (35). We found that variation in daily FMR was primarily influenced by positive relationships with body mass (daily FMR = 0.0002 × mass$^{2.41}$, R^2 = 0.91, P < 0.001, n = 9 bears) (Fig. 3A),

movement rate (daily FMR = 167.3 × rate + 153.0, R^2 = 0.82, P < 0.001, n = 9 bears) (Fig. 3B), and activity rate derived from video collars (daily FMR = 336.73 × activity + 180.5, R^2 = 0.60, P = 0.01, n = 9 bears) (Fig. 3C). We found a positive but nonsignificant relationship between activity rate derived from accelerometers and daily FMR (R^2 = 0.56, P = 0.09, n = 6 bears). We further found a positive relationship between overall FMR and total distance traveled (overall FMR = 0.006 × distance + 1.5, R^2 = 0.78, P = 0.003, n = 8 bears) (Fig. 3D). These relationships suggest that basal metabolism, locomotion, and activity were the primary drivers of energy expenditure for the polar bears in our study. This reinforces that there is a substantial cost of locomotion in polar bears relative to other quadrupedal mammals, as
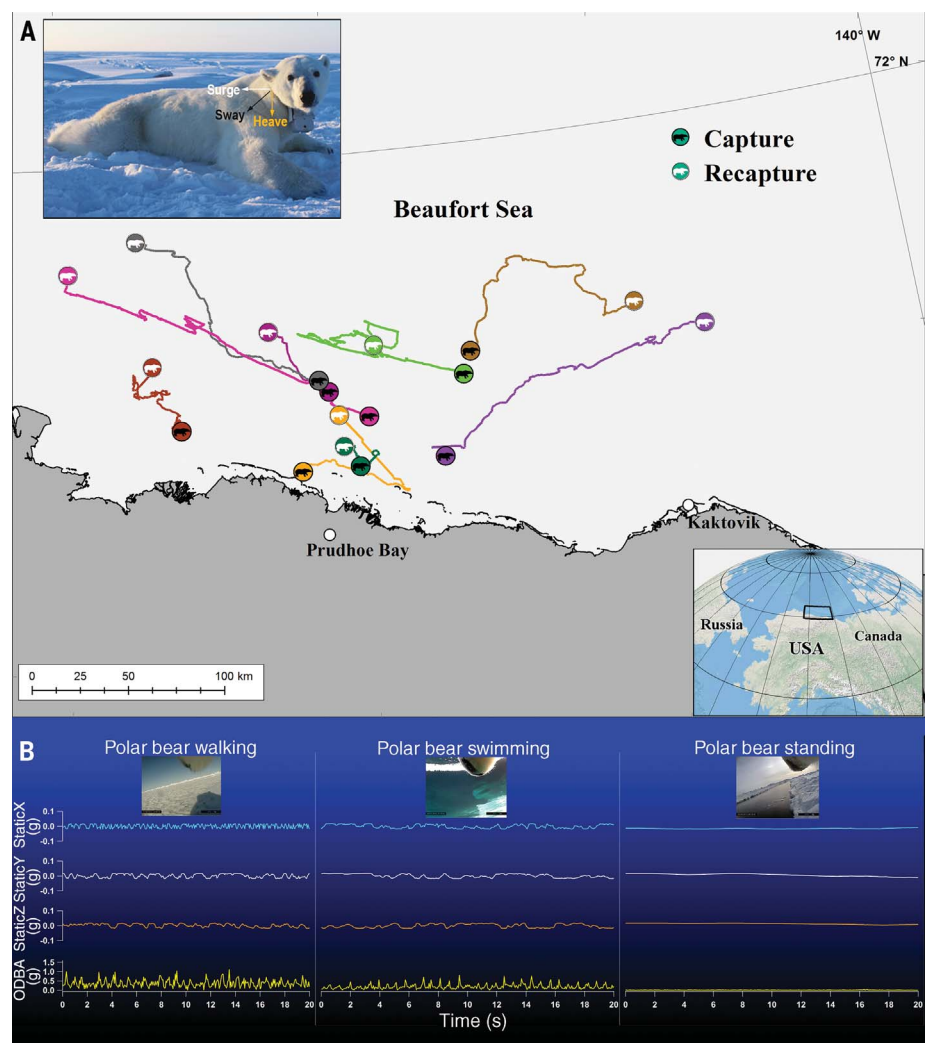

Fig. 1. Field movements and accelerometer signatures of polar bears in April 2014 to 2016. (**A**) Capture and recapture locations and GPS movement paths of nine female polar bears dosed with DLW and equipped with GPS-equipped video camera collars and archival loggers with triaxial accelerometers and conductivity sensors. Gray area denotes land; white area shows sea ice cover. (Inset) Orientation of the accelerometer while attached to the video collar. (**B**) Accelerometer signatures of static acceleration in the surge (*x*), heave (*y*), and sway (*z*) directions and overall dynamic body acceleration (ODBA) while walking, swimming, and standing. Images show the corresponding behaviors derived from the animal-borne video camera.

Fig. 2. Relationship between body mass and RMR in polar bears and other ursids. RMR of an adult female polar bear (orange triangle, this study), compared with mean RMRs of subadult polar bears (orange circle), hibernating adult female polar bears (orange square), hibernating adult male brown bears (blue square), black bears (black circle), hibernating black bears (black square), adult and subadult panda bears (green circle), and female sloth bears (purple circle). Sources are available in the supplementary materials. The dashed line is the allometric regression for RMR in vertebrate-eating carnivores (20). The solid line is the allometric regression for RMR in eutherian mammals (21). (**Inset**) The adult female bear resting in the metabolic chamber from the present study.
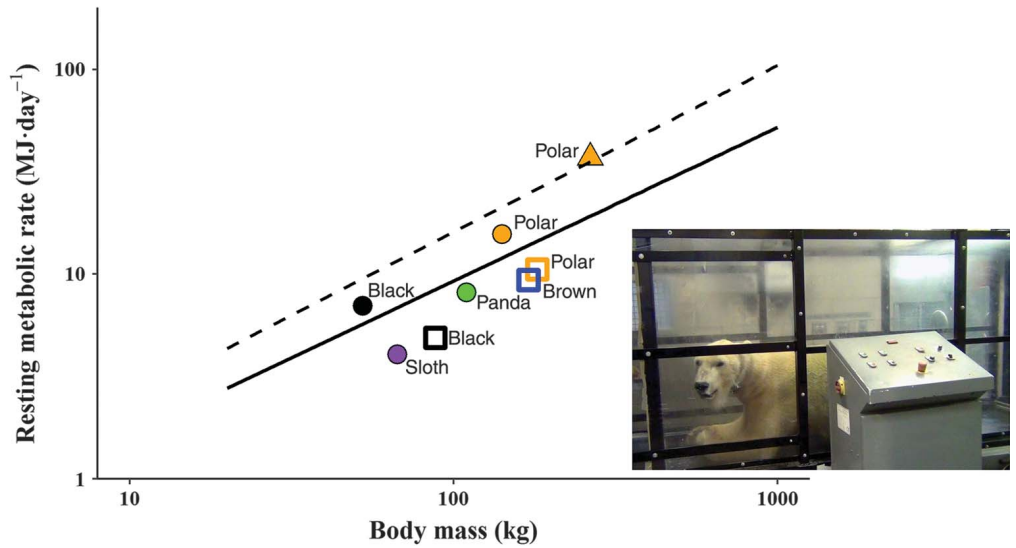
Fig. 3. Daily FMR and overall FMR in relation to body mass, movement, and activity rate of polar bears. (**A**) Mean daily FMRs of female polar bears on the sea ice in relation to body mass. The allometric regression (solid line) is compared with predicted daily FMRs for marine and terrestrial mammalian carnivores (upper dashed line) (26), and predicted daily RMRs (lower dotted line) (21). (**B**) Least squares regression (solid line) of mean daily mass-specific FMR in comparison with mean movement rate. (**C**) Least squares regression (solid line) of mean daily mass-specific FMR in comparison with mean activity rate derived from video collars. (**D**) Least squares regression (solid line) of overall mass-specific FMR in comparison with total distance moved over 8 to 11 days. Regression statistics are provided in the main text. Each point represents a single value for one bear in (A) to (D).
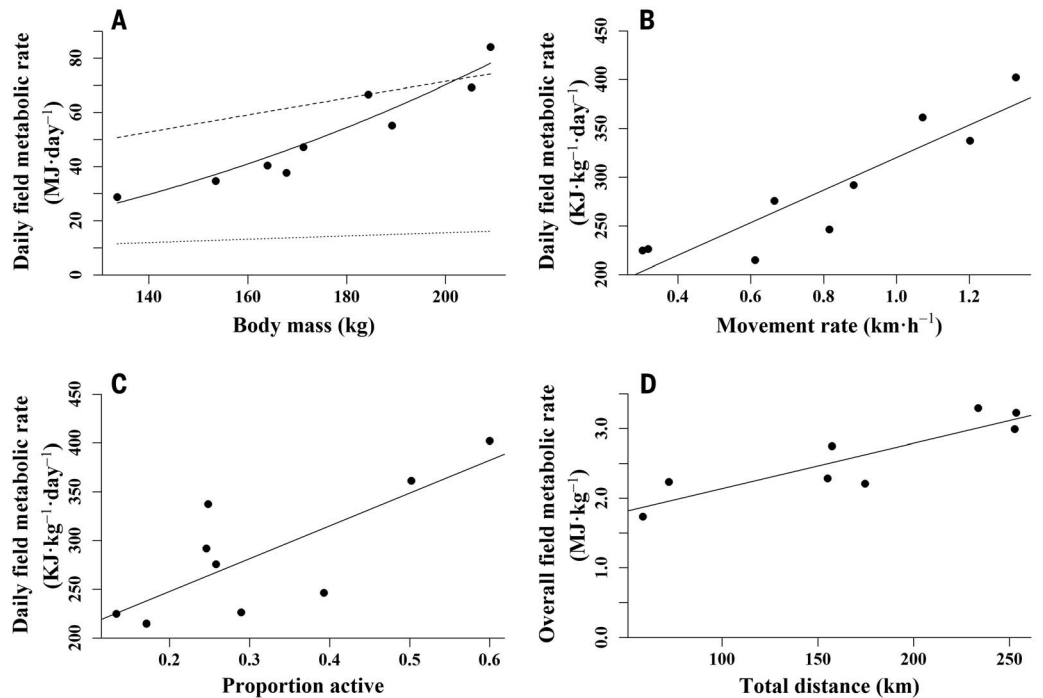
has been documented in captive treadmill studies (6). For example, bears with movement rates averaging ≥1.0 km h^{-1} (n = 3 bears) had 1.5 times greater FMRs than those of bears that moved <1.0 km h^{-1} (n = 6 bears) (Fig. 3B).
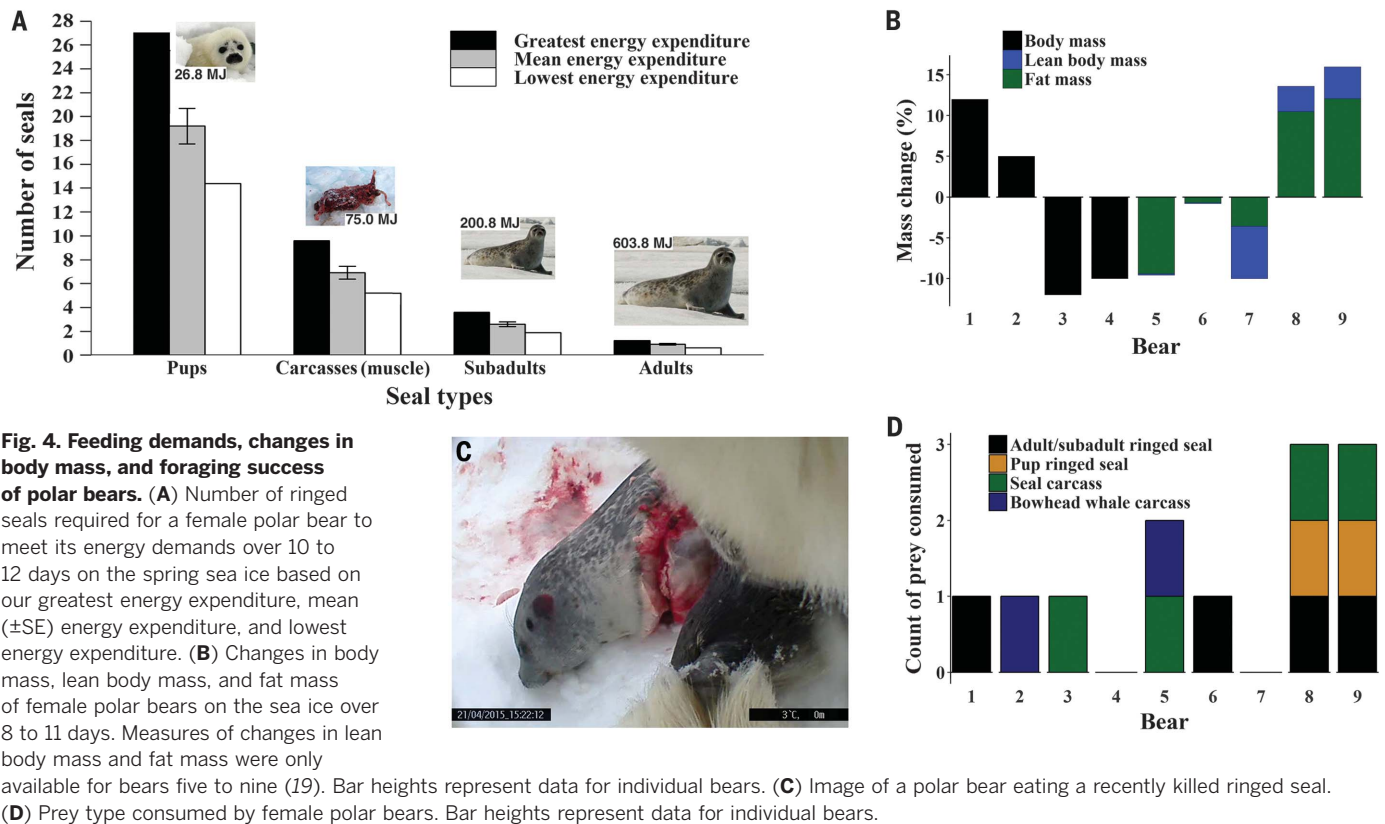
Admittedly, the activity levels and FMRs in this study may be biased low owing to the effects of recovery post-capture. On the basis of movement rate and activity sensor data, recovery post-capture for polar bears may last 2 to 3 days (36). Although one bear in this study successfully caught and ate an adult or subadult ringed seal less than 24 hours after being collared (fig. S2B) (19), most bears exhibited lower activity rates during the first 24 hours after capture (fig. S3) (19). Hence, the FMRs and activity budgets presented in this study should be considered conservative levels for free-ranging polar bears.

We found that polar bears in the spring exhibit greater energetic demands than those of previous predictions (13, 14) both for maintenance functions and locomotion. Similar to other marine mammals, polar bears likely transitioned to the marine ecosystem to take advantage of abundant prey resources (1) despite the increased energetic costs required for a marine and carnivorous existence (37). These demands necessitate access to high-energy-content prey in the form of ringed and bearded seals (*Erignathus barbatus*).

More than half of the bears in this study lost body mass, meaning that over the period of observation, their energy demand exceeded

Fig. 4. Feeding demands, changes in body mass, and foraging success of polar bears. (**A**) Number of ringed seals required for a female polar bear to meet its energy demands over 10 to 12 days on the spring sea ice based on our greatest energy expenditure, mean (±SE) energy expenditure, and lowest energy expenditure. (**B**) Changes in body mass, lean body mass, and fat mass of female polar bears on the sea ice over 8 to 11 days. Measures of changes in lean body mass and fat mass were only available for bears five to nine (*19*). Bar heights represent data for individual bears. (**C**) Image of a polar bear eating a recently killed ringed seal. (**D**) Prey type consumed by female polar bears. Bar heights represent data for individual bears.

that gained by consuming prey. Although we cannot assess the effects of post-capture recovery on our observed foraging rates, previous researchers reported that 42% of adult female polar bears in the Beaufort Sea during the spring from 2000 to 2016 had not eaten for ≥7 days before capture (*38*). This rate of fasting was 12% greater than measurements from 1983 to 1999 (*38*), suggesting that spring ice conditions are affecting prey availability for polar bears even before the summer open water period. Additionally, access to optimal habitats (annual ice over the continental shelf) is expected to and in some areas has already declined as a result of climate change (*39*, *40*). Survival rates of cubs, body condition of adult females, body size of young, litter mass, and yearling numbers have also exhibited declines in some regions of the Arctic (*41*, *42*). Together with our data on the cost of activity and energy acquisition (Figs. 3 and 4), these studies suggest that an increasing proportion of bears are unable to meet their energy demands. Our results indicate that further increases in activity and movement resulting from declining and increasingly fragmented sea ice are likely to increase the demand side of the energy balance ratio (*43*). Inherently high energy demands create a physiological constraint that makes it difficult for polar bears to compensate for both increases in activity and declines in the availability of energy-dense prey as habitats become more fragmented (*44*). Hence,

increases in movement and activity rates mediated by the loss of sea ice habitat are likely to have negative cascading effects on polar bear reproductive success and, ultimately, their populations.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S3
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Movies S1 to S4

Science

High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear

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A demanding lifestyle

Polar bears appear to be well adapted to the extreme conditions of their Arctic habitat. Pagano *et al.*, however, show that the energy balance in this harsh environment is narrower than we might expect (see the Perspective by Whiteman). They monitored the behavior and metabolic rates of nine free-ranging polar bears over 2 years. They found that high energy demands required consumption of high-fat prey, such as seals, which are easy to come by on sea ice but nearly unavailable in ice-free conditions. Thus, as sea ice becomes increasingly short-lived annually, polar bears are likely to experience increasingly stressful conditions and higher mortality rates.

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