ORGANISMAL BIOLOGY

Out of balance in the Arctic

Polar bears have high energy requirements that rise further as a result of climate change

By **John P. Whiteman**

As human activities lead to rising greenhouse gas concentrations in Earth's atmosphere, less incoming solar energy is released back into space, causing a net energy gain that increases global temperatures. The consequence of climate change for polar bears can likewise be understood in terms of an energy imbalance. Sea ice melting reduces the opportunities for polar bears to capture seals (see the photo), leaving them at risk of expending more energy in the pursuit of food than they can obtain. The magnitude of this imbalance is determined by their rate of energy use. On page 568 of this issue, Pagano *et al.* (*1*) quantify the energy expense of wild polar bears and show that it is higher than previously estimated.

Animal energy use is typically described by two terms. The resting metabolic rate (RMR) includes the energy cost of basic organismal functions, such as blood circulation and breathing. The field metabolic rate (FMR) includes RMR as well as the energy cost of additional activities, such as movement and foraging. Because energy balance influences whether an animal survives and reproduces, RMR and FMR are critical variables in ecology and conservation. But they are notoriously difficult to quantify for large, mobile animals, particularly in remote habitats.

Polar bears look for food onshore in East Greenland, August 2016. The species needs sea ice as a platform to capture energy-rich prey, particularly seals. Polar bear population trends currently vary across the Arctic, but scientists expect broad declines if sea ice loss continues.

Scientists have previously estimated polar bear energy requirements by calculating RMR with predictive body mass–based equations derived from other species and then multiplying RMR by a constant to yield FMR (*2*). In another study, a researcher extrapolated field observations of seal kill rates to estimate the energy intake and FMR of polar bears (*3*). These and other studies assumed that polar bears can spontaneously reduce their RMR during food deprivation, which would be beneficial while searching for sparsely distributed seals. A recent study,

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however, found that polar bear energy expense does not substantially decline during fasting (*4*), leaving the magnitudes of both their RMR and FMR uncertain.

In their study, Pagano *et al.* measured rates of oxygen consumption and carbon dioxide production in polar bears; these variables can be converted to energy use. First, the researchers assessed RMR by training a zoo polar bear to sit quietly in a chamber while its oxygen consumption was measured. Next, they quantified FMR in nine free-ranging bears on sea ice near the northern coast of Alaska, USA, by using doubly labeled water. To do so, the authors first captured the bears and injected them with water labeled with heavy stable isotopes ($^2H_2{}^{18}O$); they also collected a baseline blood sample. About 10 days later, they recaptured the bears and took a second blood sample. In the interim, the injected ^{2}H left the body in water molecules (for example, through urination), whereas the ^{18}O left the body in both water and exhaled CO_2 because oxygen atoms readily exchange between H_2O and CO_2 in the blood. As a result, the difference in decline of ^{18}O and ^{2}H between sampling events represents the CO_2 production rate, which in turn reflects FMR.

FMRs of the free-ranging bears were on average 1.6 times higher than previous estimates (see the figure) but were consistent with expectations for mammals that mainly consume other vertebrates; these mammals expend more energy than those consuming vegetation or mixed diets (*5*). Similarly, the zoo bear had a relatively high RMR, matching expectations for a carnivore. Although the mechanism for the high energy cost associated with meat-eating is unclear (*6*), these findings emphasize that polar bears have evolved as hunters, particularly of fat-rich marine mammal prey. This distinguishes them from other bear species, which include herbivores, insectivores, and omnivores. Polar bear activity patterns are also different from those of other bears: On average, the individuals sampled by Pagano *et al.* were active for 34% of their time, making them more similar to large terrestrial carnivores (39%) than to other bear species (50 to 60%) (*7*).

The high energy requirements of polar bears corroborate previous hypotheses that most terrestrial Arctic habitats, lacking prey as energy-rich as marine mammals, cannot provide enough food for polar bears driven to shore by loss of sea ice (*8*). In addition, Pagano *et al.*'s results demonstrate that polar bears do not reduce their metabolic rate when food is scarce (*4*). Four of the nine bears lost ≥10% of their body mass during the days between blood sampling events; at least one of these bears lost substantial lean tissue (structural proteins such as muscle) as well as fat (the primary form of energy storage). These bears nevertheless had high FMRs.

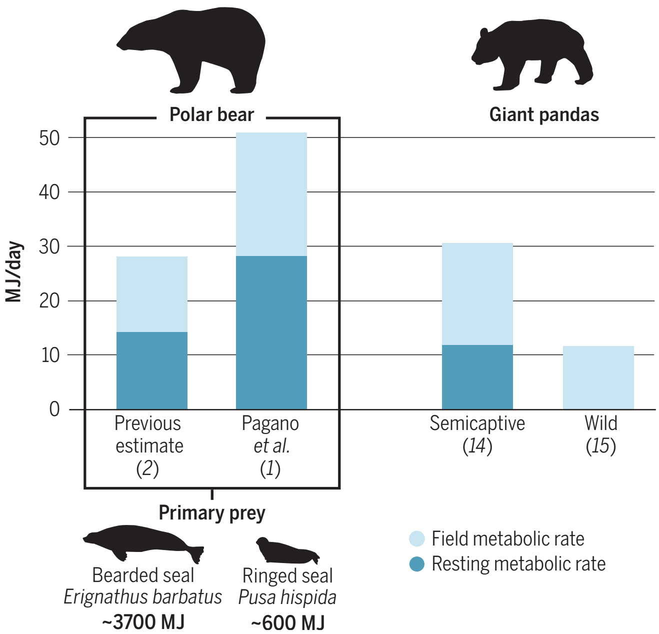
Pagano *et al.*'s findings refine our understanding of how polar bears are affected by environmental change in the Arctic. Longer periods of ice melt are lengthening the time during which the bears must endure food deprivation in summer. Molnár *et al.* have previously used anatomical models of energy storage and body mass change over time to estimate that starvation mortality of adult male bears would increase from 6 to 48% if summer fasting were extended from 120 days to 180 days (*9*). Such models can now be modified to include empirical FMR estimates. Further, thinner sea ice drifts faster, and polar bears have had to increase their movement rates in order to remain in their preferred habitat, incurring higher energy costs (*10*). These costs can now be modeled more precisely because of the strong linear relationship between movement rate and FMR reported by Pagano *et al.*

The data also help to resolve why the population-level response of polar bears to sea ice loss varies by region. For example, two Alaskan subpopulations of polar bears have recently experienced substantial ice loss, but only one of them is declining thus far (*11*). High and relatively inflexible RMRs and FMRs for polar bears suggest that population responses are mainly driven by local, ecological factors, such as primary productivity or overlap of seal distribution with remaining sea ice habitat. Ice loss, if unabated, will eventually cause the extinction of polar bears in the wild (*12*), but continued research is needed to understand the climate-related pressures that polar bears face. Such data-driven explanations of the biological consequences of climate change are critical for public understanding and action (*13*).

Important questions remain regarding the energy balance of polar bears. Pagano *et al.* captured free-ranging individuals during spring, when new seal pups and attentive adult seals are most vulnerable to predation. During winter, polar bear activity declines, and some individuals retreat into "shelter dens" for days to weeks at a time (excluding pregnant females, which hibernate). It is unknown whether there is a concurrent seasonal reduction in FMR. Energy expense in late winter is critical because body condition reaches an annual low in this period, making it the most likely time for climate change–related mortality. In addition, Pagano *et al.* sampled bears without dependent cubs, leaving the cost of rearing young (such as lactation) to be quantified. ■

Energy balance of adult female polar bears

A 175-kg polar bear needs far more energy than a herbivorous giant panda (*Ailuropoda melanoleuca*), scaled to the same body mass. Polar bears therefore require access to high-energy food sources, particularly pagophilic (ice-loving) seals.



GRAPHIC: N. CARY/SCIENCE

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