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SUPPLEMENTARY MATERIALS

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ANIMAL PHYSIOLOGY

Summer declines in activity and body temperature offer polar bears limited energy savings

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Polar bears (*Ursus maritimus*) summer on the sea ice or, where it melts, on shore. Although the physiology of “ice” bears in summer is unknown, “shore” bears purportedly minimize energy losses by entering a hibernation-like state when deprived of food. Such a strategy could partially compensate for the loss of on-ice foraging opportunities caused by climate change. However, here we report gradual, moderate declines in activity and body temperature of both shore and ice bears in summer, resembling energy expenditures typical of fasting, nonhibernating mammals. Also, we found that to avoid unsustainable heat loss while swimming, bears employed unusual heterothermy of the body core. Thus, although well adapted to seasonal ice melt, polar bears appear susceptible to deleterious declines in body condition during the lengthening period of summer food deprivation.

The current rate of Arctic sea-ice loss, unprecedented in at least the past several thousand years, is outpacing predictions and accelerating (1). This raises concerns about the persistence of polar bears (*Ursus maritimus*) (2), which hunt on the surface of the sea ice, most successfully between April and July (3), when ringed seals (*Pusa hispida*) use this substrate for rearing pups and molting (4). Between August and October, hunting can be poor (5) as seals reduce ice surface time (4). Additionally, in about two-thirds of the polar bear range (6), seals become largely pelagic as ice retreats from the continental shelf (7, 8). Some polar bears spend this period on shore, where foraging is also usually limited (9).

To reduce the loss of body condition during summer food deprivation, shore bears purportedly enter a state of lowered activity and resting metabolic rate similar to winter hibernation but without denning (10). This “walking hibernation” could partially compensate for the nega-

tive impacts of extended ice melt (11). However, in western Hudson Bay, Canada, shore bears lose body mass at a rate indicative of typical, rather

than hibernation-like, metabolism (12). The physiological state of bears that follow the retreating sea ice into the central Arctic basin in summer is unknown. In addition, recent sea-ice loss may be increasing the frequency of long-distance swims by polar bears (13), during which they risk losing over 10 times more heat than they produce (supplementary text) because their fur loses 90% of its insulation value when wet (14), and their subcutaneous fat does not provide blubber-like insulation (15).

To understand polar bear responses to these challenges of summer ice melt, we investigated activity on shore (2008 and 2009) and on ice (2009) in the Beaufort Sea (Fig. 1) by affixing telemetry transmitters and activity loggers (16) to 25 females (mean age = 10 years ± 1 SE, age range = 4 to 20 years) and one male (age 3). We recorded temperatures of the body core (an index of metabolic rate) (17) and periphery by implanting loggers into the abdomens (core) of 10 bears (nine females, mean age = 11 years ± 2 SE, age range = 3 to 23 years; one male, age 6) and the rumps (periphery) of seven other individuals (six females, mean age = 9 years ± 2 SE, age range = 5 to 20 years; one male, age 2).

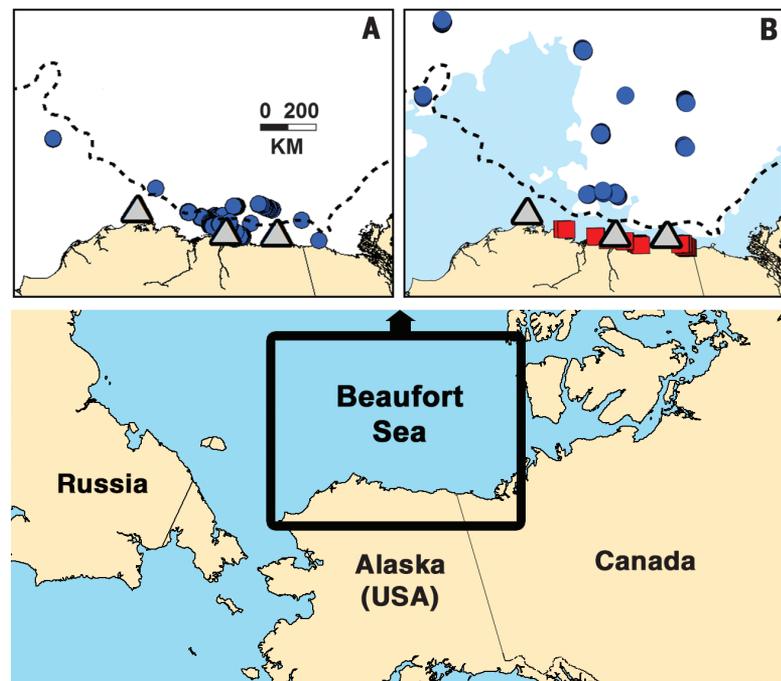


Fig. 1. The western Arctic on (A) 11 May 2009 and (B) 31 August 2009. Locations are shown for ice polar bears (blue circles), shore polar bears (red squares), and whale carcasses (triangles). The 300-m depth contour is shown as a dashed line. Sea ice is shown in white.

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Bears on shore and ice exhibited similar activity patterns (Fig. 2A and tables S1 and S2; in table S1, shore data from 2008 and 2009 were pooled for lack of difference). Their time spent active peaked at ~25% between May and July, then fell to 12 to 22% between August and October (Fig. 2A), remaining greater than the values of 1 to 2% previously observed during winter hibernation (18). The maximum activity level we measured (~25%) is approximately half that observed in all other bear species (19), perhaps reflecting polar bears' specialization for hunting large vertebrate prey (3). The high energy costs of finding and subduing such prey can be reduced by ambush tactics (20), such as still-hunting at seal breathing holes (3).

Although bears on shore and ice were similarly active between August and October, movement rates were higher for ice bears (Fig. 2B and table S1), potentially because the sea ice underfoot was drifting at 0.30 to 0.60 m/s (21). The proportion of rapid movement rates (>0.33 m/s) recorded when ice bears were resting (i.e., motionless for ≥98% of the previous half hour) (16) increased in late summer (Fig. 2C), suggesting that as bears reduced their activity, their movement rates increasingly reflected ice drift.

We did not find support for the hypothesis that lowered activity of shore and ice bears is a response to decreased food availability. For ice bears, location relative to primary seal habitat over the continental shelf (7, 8) was a poor predictor of activity (mean model coefficients overlapped with zero; $n = 23$ bears) (table S3). This result suggests that additional factors determine seal distribution (e.g., fine-scale variation in productivity) (8) or their availability as prey (e.g., time spent on the ice surface) (4). Similarly, access to concentrated food resources for shore bears [i.e., locations within 500 m of bowhead whale (*Balaena mysticetus*) carcasses from Inuit subsistence harvest (table S4)] was not associated with activity levels ($n = 7$ bears) (table S3).

Bears may reduce activity to avoid heat stress in summer, because their large body size and low ratio of surface area to volume hinder heat dissipation. In a previous study, captive polar bears became hyperthermic while walking on treadmills at speeds ≥1.6 m/s when air temperature was ≥-5°C (22). However, air temperature in our study (daily means: -14.8° to 15.1°C) was unrelated to activity of shore bears ($n = 12$ bears) (table S3). Also, only 31 of our 61,882 measurements of movement rate (shore and ice combined; $n = 25$ bears) were ≥1.6 m/s, indicating that free-ranging bears seldom walk that rapidly. Thus, locomotion-induced heat stress is probably rare and insufficient to explain the reduction in summer activity.

Core body temperatures (monthly means of smoothed data) (16) did not differ between shore and ice bears during summer (Fig. 2D, table S1, and fig. S1), suggesting that all bears had similar nonhibernating, resting metabolic rates (fig. S2A). Mean core temperatures of ice bears gradually declined from May (37.3°C) to September (36.6°C)

(Fig. 2D). It is unclear whether a similar trend occurred in shore bears, because they were implanted with loggers in August.

These gradual temperature declines correlated with activity (mean $r = 0.31$, $n = 9$ bears) (table S5) (16) and may have been associated with fasting (5). Fasting can cause progressive reduction in body temperature of ~1°C in mammals (23, 24), corresponding with up to ~20% decreases in whole-body metabolic rate (23–25). However, the reduction in mass-specific metabolic rate is smaller and sometimes nonexistent after the loss of metabolically active tissue is considered (24). Unfortunately, we were unable to assess mass changes because we captured bears in spring before they reached peak mass (table S6). Reduced insulation from thinning of fur and subcutaneous fat could also cause temperature declines, although warm summer conditions could counteract insulation loss. Hence, gradual declines in the summer core temperature of polar bears suggest reductions in energy expenditure typical of food-deprived mammals (24).

Data from one pregnant female that retained her logger through January provide evidence that polar bears in maternal dens exhibit hibernation core temperatures in winter. In contrast to the gradual declines observed in summer, her core temperature abruptly fell to ~35°C after 28 November (Fig. 2D and fig. S2B), as would be expected after parturition (3, 26). Such low temperature presumably reflects a 50 to 80% reduction in metabolic rate during winter hibernation, similar to that seen in other ursids (fig. S2A) (26, 27).

Core temperatures, like movement rates, indicated that polar bears did not experience heat stress in summer. When walking on a treadmill at ≥1.6 m/s, captive polar bears frequently exhibited temperatures >39.0°C, including uncontrolled rises to >40.0°C, leading to the conclusion that they store excess heat and are inefficient walkers (22). However, only 18 of our 27,843 measurements ($n = 10$ bears) were >39.0°C and none were >40.0°C. This suggests that polar bear heat storage and locomotion efficiency should be reassessed and that polar bears thermoregulate effectively during summer.

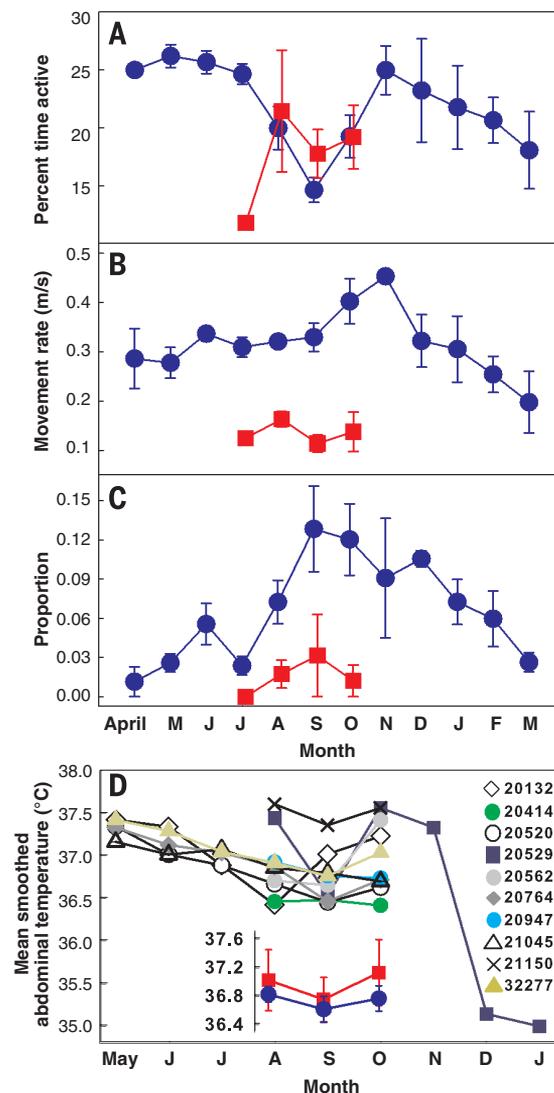


Fig. 2. Polar bear activity and abdominal temperature. (A and B)

Grand means (\pm SE) of activity and movements for bears on sea ice (circles) and on shore (squares), April to March (2008–2010). (C) Proportion of movement rates >0.33 m/s recorded when bears were inactive. (D) Individual means (\pm 95% CI) from May to October for ice bears (except location unknown for bear 20132) and from August to October for shore bears. The inset depicts grand monthly means from August to October on ice (circles) and on shore (squares). Sample sizes are in table S7 ($n = 1$ for July on shore); raw data are in fig. S1.

We also observed brief bouts of cold core temperatures ($<35.0^{\circ}\text{C}$, typically ≤ 12 hours) as low as 22.3°C . These temperature changes were too rapid (up to $\pm 5.0^{\circ}\text{C}$ per hour) to represent fluctuations in whole-body metabolic rate. Such bouts occurred in five of five shore bears and one of four ice bears. Similar peripheral temperature changes were recorded by rump loggers in six shore bears and one ice bear, although maximum hourly swings were greater for the periphery (means: $+11.8^{\circ}\text{C}$ and -10.4°C) than for the core (means: $+5.0^{\circ}\text{C}$ and -5.0°C) (supplementary text).

It is unlikely that cold bouts of peripheral and core temperatures reflected consumption of ice or lying on it, as some occurred during above-freezing air temperature when sea ice was absent. Instead, cold bouts appeared to be caused by two modes of regional heterothermy: (i) cool-

ing the body periphery during inactivity and (ii) cooling the periphery and part of the core while swimming (Fig. 3, A to D and fig. S3). Supporting this distinction, peripheral temperatures fell below 35.0°C during both inactivity (49 of 800 measurements, $n = 3$ bears) and swimming (572 of 741 measurements, $n = 3$ bears). In contrast, core temperatures fell below 35.0°C only during swimming (6 of 11 measurements, $n = 1$ bear) (supplementary text) and never during inactivity (0 of 353 measurements, $n = 1$ bear). Furthermore, cold peripheral temperatures ($<35.0^{\circ}\text{C}$) were associated with lower activity and warmer collar temperatures (i.e., when the bear curled up, warming the collar sensor) than were cold core temperatures (Fig. 3, E and F).

Regional heterothermy of the body core is unusual (17) and may minimize heat loss while

swimming. Immersed polar bears probably reduce skin temperature to several degrees above the surrounding water (supplementary text) (15), similar to seals (28). Our data suggest that bears maintain an internal thermal gradient by temporarily cooling the outermost tissues of their core to form an insulating shell. A similar process occurs in diving king penguins (*Aptenodytes patagonicus*), another polar endotherm without blubber (29). Control of this process is probably active (e.g., via vasoconstriction), because abdominal loggers cooled more quickly than is possible passively, and temperatures were subsequently regulated (Fig. 4 and supplementary text). This regional heterothermy may represent an adaptation to long-distance swims (13), although its limits remain unknown. One of our bears survived a 9-day swim, but when recaptured 7 weeks later, she had lost 22% of her body mass and her cub (30).

Sea-ice loss (1) increasingly limits spring and summer hunting opportunities for polar bears in parts of their range (2). In the Beaufort Sea and elsewhere (2, 31), this has reduced the energy stores available for bears during subsequent food deprivation (2, 5). We found that both core temperature and activity remained above values observed during winter hibernation. The gradual declines in core temperature during summer suggest a typical mammalian response to fasting, which offers limited to no energy savings based on mass-specific metabolic rates (24). Thus, our data indicate that bears cannot use a hibernation-like metabolism to meaningfully prolong their summer period of fasting and reliance on energy stores. In conjunction with theoretical models linking normal metabolic rate to depletion of stored energy and mortality (32), our findings suggest that bears are unlikely to avoid deleterious declines in body condition, and ultimately survival, that are expected with continued ice loss and lengthening of the ice melt period (2).

Fig. 3. Body temperature of a swimming polar bear.

(A) Hourly abdominal (core) temperature of bear 20414 in 2009. A bout of cold temperatures (arrow) is expanded in (B). (C) Temperatures from the collar and a weather station 110 km away during the same cold bout. (D) Collar acceleration scores during the same cold bout. (B) through (D) are divided into time periods 1 to 5. In period 1, stationary locations and high collar temperatures indicate resting on shore and covering the collar. In 2, locations were offshore, collar temperatures were consistent with immersion, and acceleration suggests swimming. In 3 through 5, locations indicate walking along the coast, resting, then walking again. (E) Mean activity ($\pm 95\%$ CI) measured during bouts of cold temperatures ($<35.0^{\circ}\text{C}$) recorded from abdominal ($n = 69$, three bears pooled) and rump ($n = 259$, one bear) loggers. (F) Mean collar temperature ($\pm 95\%$ CI) measured during bouts of cold temperatures ($<35.0^{\circ}\text{C}$) recorded from abdominal ($n = 68$, three bears pooled) and rump ($n = 829$, six bears pooled) loggers.

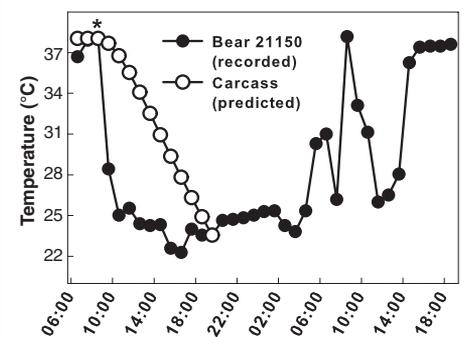
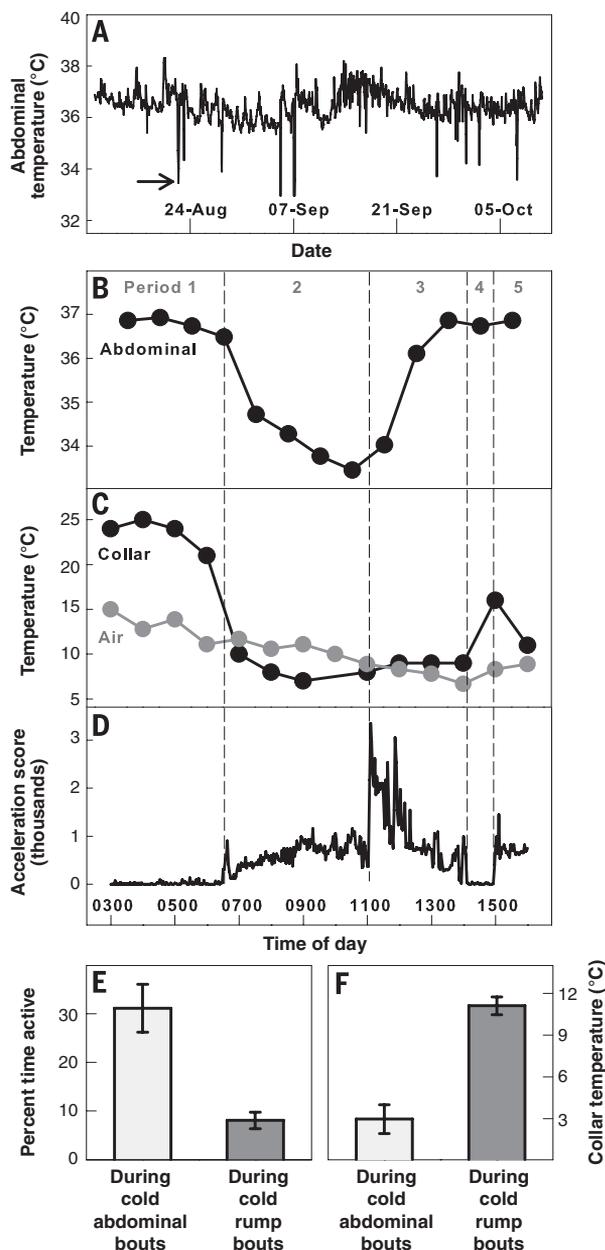


Fig. 4. Cooling curves of a polar bear. Hourly abdominal (core) temperatures [06:00 (UTC -08:00) on 2 October to 18:00 on 3 October 2009] represent swimming based on sparse location data (solid circles). Predicted intraperitoneal temperatures (open circles) represent cessation of heat production (death) at the asterisk and subsequent immersion in 4°C water (supplementary text).

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SUPPLEMENTARY MATERIALS

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THERMAL PHYSIOLOGY

Keeping cool: Enhanced optical reflection and radiative heat dissipation in Saharan silver ants

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Saharan silver ants, *Cataglyphis bombycina*, forage under extreme temperature conditions in the African desert. We show that the ants' conspicuous silvery appearance is created by a dense array of triangular hairs with two thermoregulatory effects. They enhance not only the reflectivity of the ant's body surface in the visible and near-infrared range of the spectrum, where solar radiation culminates, but also the emissivity of the ant in the mid-infrared. The latter effect enables the animals to efficiently dissipate heat back to the surroundings via blackbody radiation under full daylight conditions. This biological solution for a thermoregulatory problem may lead to the development of biomimetic coatings for passive radiative cooling of objects.

The silver ants of the Sahara desert, *Cataglyphis bombycina*, inhabit one of the hottest terrestrial environments on Earth, where they occupy the ecological niche of a “thermophilic scavenger” (1). In wide-ranging foraging journeys, they search for corpses of insects and other arthropods that have succumbed to the thermally harsh desert conditions, which they themselves are able to withstand more successfully. On hot summer days, they may reach maximal foraging activities when temperatures of the desert surface are as high as 60° to 70°C and their body temperatures measured as “operative environmental temperatures” are in the range of 48° to 51°C (2, 3). In order to survive under these conditions, occasionally the ants must unload excess heat by pausing on top of stones or dry vegetation, where, because of the steep temperature gradient above the sand surface, they encounter considerably lower temperatures. Under the midday sun of a summer day, the ants may resort to this thermal respite (cooling off) up to 70% of their entire foraging time (3). In keeping their body temperature below their critical thermal maximum of 53.6°C (4), they need not only to reduce heat absorption from the environment but also to be able to efficiently dissipate excess heat, so that they can minimize the amount of time spent in thermal refuges.

As we showed, through a series of optical and thermodynamic measurements, full-wave simulations, and heat-transfer modeling, a dense array of triangularly shaped hairs, characteristic of *Cataglyphis bombycina*, enables the ants to main-

tain lower body temperatures by (i) reflecting a large portion of the solar radiation in the visible and near-infrared (NIR) range of the spectrum and (ii) radiating heat to the surrounding environment by enhancing the emissivity in the mid-infrared (MIR), where the blackbody radiation spectrum of the ant's body culminates. The thermoregulatory solutions that the silver ants have evolved to cope with thermally stressful conditions show that these animals are able to control electromagnetic waves over an extremely broad range of the electromagnetic spectrum (from the visible to the MIR) and that different physical mechanisms are employed in different spectral ranges to realize an important biological function.

Specimens of *Cataglyphis bombycina* collected in Tunisia (34°10'N, 08°18'E) were used for all of the optical and thermodynamic measurements. In these ants, the dorsal and lateral sides of the body have a silvery glare (Fig. 1A) and are covered by dense and uniform arrays of hairs (Fig. 1B and fig. S4). As scanning electron microscopy (SEM) images show, the hairs, which gradually taper off at the tip, are locally aligned in the same direction (Fig. 1C). Their most remarkable structural feature is the triangular cross-section characterized by two corrugated top facets and a flat bottom facet facing the ant's body (Fig. 1, D and E). Cross-sectional views obtained by focused ion beam (FIB) milling show that the gap between the bottom hair facet and the cuticular surface also varies but is generally larger than a few hundred nanometers.

Optical reflectivity measurements of ant specimens were obtained with two Fourier transform spectrometers, one collecting spectra in the visible and NIR (wavelengths from 0.45 to 1.7 μm) and the other in the MIR (wavelengths from 2.5 to 16 μm). The visible and NIR measurements showed that hemispherical reflection [i.e., the sum of specular and diffuse reflection collected through an integrating sphere (2)] is substantially enhanced

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Summer declines in activity and body temperature offer polar bears limited energy savings

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Not that unusual after all

As polar ice recedes, polar bears are facing a changed habitat with reduced summer foraging opportunities. It has been hypothesized that they might be able to resist summer food shortages by reducing their metabolic needs in a sort of "walking hibernation." Whiteman *et al.* monitored energy expenditure in polar bears both on and off the ice and found energy reductions, but that these were more akin to normal mammalian fasting levels. Thus, it appears that polar bears have no energetic protections against reduced summer food supplies and will face increasing starvation threats if summer foraging habitats continue to decline.

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