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Chapter 12
Polar Bear Behavior: Morphologic and Physiologic Adaptations

John P. Whiteman

Abstract Polar bears possess morphologic and physiologic characteristics that reflect their terrestrial lineage as members of the bear family (Ursidae) as well as adaptations to the Arctic marine environment. Among marine mammals, they are the least adapted for aquatic life. They exhibit substantial seasonality in body mass, body condition, and many physiological functions, reflecting the annual cycle of both their Arctic sea ice habitat and the availability of their main prey, ringed seals. This hypercarnivorous diet has likely influenced the polar bear's craniodental morphology and nutritional physiology. Similar to other marine mammal predators, polar bears exhibit a relatively high resting metabolic rate (RMR) and field metabolic rate (FMR). The polar bear skeleton is well adapted for walking, rather than tree-climbing, and to a lesser degree, for swimming. The large feet provide secure traction on sea ice (aided by sharp claws) and propulsion in the water. Their reproduction, winter hibernation (by pregnant females), and sensory systems resemble those of other bears. Future research should focus on nutrient recycling during fasting, adaptation to a high-fat diet, susceptibility to pathogens, and assessment of the fitness consequences of ongoing sea ice loss and chemical contamination of their habitat.

Keywords Climate change · Contaminants · Craniodental · Creatinine · Disease · Fasting · Fat · Hibernation · Metabolism · Morphology · Nutrition · Physiology · Polar bear · Sea ice · Sensory · Thermoregulation · Urea

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12.1 Introduction

At first glance, polar bears (*Ursus maritimus*) stand out as unique among marine mammals because of their strong resemblance to the other seven extant bear species (family Ursidae), all of which are terrestrial. However, polar bears have rapidly evolved to occupy a novel niche as apex predators hunting from the surface of the Arctic sea ice. Indeed, they are powerful swimmers and can make short, shallow dives when pursuing prey (see Chap. 16). The entirety of polar bear natural history unfolds on the sea ice and in adjacent coastal ecosystems, but their fossil record is sparse because most die at sea and their remains sink into the ocean (Ingolfsson and Wiig 2009). The features that distinguish polar bears since they diverged from brown bears (*Ursus arctos*) reflect their adaptation to the sea ice habitat and to a hypercarnivorous diet of marine mammal prey (see Chap. 11; Hailer et al. 2012; Liu et al. 2014).

In this chapter, I discuss the most prominent organismal characteristics of polar bears, often in comparison with other bear and marine mammal species. Because there is a close association between the form and function of an animal and the abiotic and biotic components of its environment, these discussions will be interwoven with references to polar bear behavior and ecology. In addition, because this chapter is written in the early twenty-first century—a period of swift and dramatic change in the Arctic from global warming, pollution, and other anthropogenic effects—I also consider how sea ice loss and environmental change are affecting polar bear morphology, physiology, and behavior.

12.2 Morphology

12.2.1 Temporal and Spatial Variation in Morphometrics

The global population of polar bears occupies the Arctic and sub-Arctic and is divided into 19 subpopulations primarily based on movements, although there are varying degrees of restricted gene flow across subpopulation boundaries (see Chap. 11; Paetkau et al. 1999; Peacock et al. 2015; Malenfant et al. 2016). Growth rates, body sizes, and the relationship between body mass and length vary among subpopulations (Durner and Amstrup 1996; Cattet et al. 1997; Derocher and Stirling 1998; Derocher and Wiig 2002). This variation is related to regional ecosystem productivity and diet, but genetic differences, density-dependent effects, and pollution exposure also may be important.

At birth, male and female cubs do not differ in body mass and length, but males become significantly larger during the first year of life. By the time bears reach 20 years of age, roughly the end of their prime adult years, males are approximately twice as massive as females (Derocher and Wiig 2002; Derocher et al. 2005). This dimorphism is among the largest among mammals, perhaps second only to the differences between males and females of some Pinnipedia (e.g., elephant seals [*Mirounga* spp.]) (Derocher et al. 2005). Polar bears reach 97% of their asymptotic (i.e., adult) body length between 4–6 years of age, with females usually reaching this length earlier than males (Derocher and Stirling 1998; Rode et al. 2010). Adult body length is approximately 150–250 cm for females and 200–300 cm for males (Derocher and Wiig 2002; Amstrup 2003).

Polar bears are the largest extant species of Ursidae, rivaled in body mass only by some subpopulations of brown bears (Hilderbrand et al. 1999; Swenson et al. 2007). Adult body mass generally ranges from 150–350 kg for females and 350–650 kg for males, but mass varies substantially throughout their annual cycle (Derocher and Stirling 1995; Stirling 1999; Derocher and Wiig 2002; Amstrup 2003). In general, polar bears gain mass during spring when seals (predominantly ringed seals, *Pusa hispida*) are most vulnerable to predation (because of pupping and molting) and lose or maintain mass during the remainder of the year. During summer and autumn, polar bears in some subpopulations lack access to marine mammal prey because of seasonal reductions in sea ice. These individuals tend to lose body mass as they fast or consume lower-energy terrestrial food, such as vegetation and bird eggs (Rode et al. 2015). In Western Hudson Bay (WHB), summer mass loss rates are ~0.9 kg day^{-1} for adults, ~1.1 kg day^{-1} for subadults, ~0.6 kg day^{-1} for yearlings, and ~0.3 kg day^{-1} for cubs (Derocher and Stirling 1995; Atkinson et al. 1996). These rates of mass loss, which occur when polar bears are likely consuming terrestrial food items, are nearly identical to the rates of mass loss of polar bears fasting in temporary captivity after human-wildlife conflict (Derocher and Stirling 1995; Atkinson et al. 1996; Pilfold et al. 2016). This similarity suggests that terrestrial feeding does little to offset the loss of stored energy. An important exception can occur when polar bears turn to an alternative food source that resembles their typical diet of marine mammals. For example, some polar bears remaining on land during the summer ice melt season in the Southern Beaufort Sea (SBS) maintain their body mass by scavenging carcasses of bowhead whales (*Balaena mysticetus*) deposited after human subsistence harvest (Whiteman et al. 2018).

There are no body mass data for polar bears during winter because of the difficulty of captures in the Arctic during this season, although low masses in spring suggest that polar bears reach an annual minimum in late winter (Durner and Amstrup 1996; Stirling et al. 2008). Indeed, the lipid content of adipose tissue (which is a proxy for body condition; see Sect. 12.2.4) in hunter-harvested polar bears reached an annual minimum during April–May in five subpopulations; importantly, this dataset included lipid content measurements throughout the winter (Galicia et al. 2019). Changes in body mass also depend on reproductive status. Pregnant females accrue extraordinary fat deposits and additional lean tissue before winter hibernation (see Sect. 12.5) to provide the stored energy and organic material required for gestation and lactation (Atkinson and Ramsay 1995; Atkinson et al. 1996).

Polar bear body condition is often quantified by assessing body mass relative to length, an approach that has been validated with complementary data, such as the mass of dissected skeletal muscle and lipid tissue of individual carcasses (Cattet et al. 2002). However, morphometric body condition indices depend on the consistency and accuracy of the underlying anatomical measurements and can fail to reflect subtle variation among individuals (Cattet et al. 1997; Pagano et al. 2017). Body condition has recently declined for some subpopulations of polar bears. In Southern Hudson Bay (SHB), body condition (residuals from a regression of mass versus length) of all age and sex classes declined during 1984–2009 (Obbard et al. 2016). In WHB, declines have occurred during two time periods. First, body condition (mass $\times$ length^{-2}) declined during 1981–1997 for males and for females $\geq$4 years of age (Stirling et al. 1999). Second, body condition (defined as MJ of stored energy calculated from mass and length) declined during 2004–2013 for all age and sex classes (Molnár et al. 2009; Sciullo et al. 2016). In Davis Strait (DS), body condition (chest girth as a proxy for body mass) declined during 1978–1994 for males and females $\geq$2 years of age, and this decline continued to 2007 for females but not for males (Rode et al. 2012). In Baffin Bay (BB), body condition (chest girth) declined from 1992–2010 for males and females $\geq$2 years of age (Rode et al. 2012). In the SBS, the body length of individuals $>$3 years of age declined from 1982–2006 (Rode et al. 2010). Changes in body mass over that period in the SBS were complex, including decreases for some polar bears (e.g., females of age 3–4 years or $>$8 years) and increases for others (females of age 5–8 years). In contrast to the long-term declines in body condition in some subpopulations, polar bears in the Chukchi Sea (CS) showed either no change between 1986–1994 and 2008–2011 or increases in mass (yearlings of both sexes, adult females) and length (adult females; Rode et al. 2014). Sea ice availability is a primary influence on polar bear body mass, length, and body condition, and some of these declines in body size are attributable to sea ice loss (Rode et al. 2010, 2012; Obbard et al. 2016). Other variables such as population density and local prey availability are also influential (Rode et al. 2012, 2014).

12.2.2 Craniodental Morphology and Feeding

Polar bears are the only Ursidae species that almost exclusively consume vertebrate prey, and this hypercarnivory likely has been an important selection pressure in the evolution of their skull morphology (Christiansen 2007; Figueirido et al. 2009). In comparison to the other seven extant bear species, polar bears have the unique combination of a large and convex mandible with a deep symphysis, a flattened cranium, a deep rostrum, and upwardly-positioned eye orbits (Figueirido et al. 2009). When compared to their closest relative, the brown bear, the flattened appearance of the polar bear cranium may be the most obvious distinction (Fig. 12.1). Likely as a consequence of this flattening, polar bear masticatory muscles exhibit a different morphology than those in brown bears, and the stresses from biting are more unevenly dispersed throughout the polar bear skull, creating greater potential for cranial strain and deformation (Sasaki et al. 2000; Slater et al. 2010). This suggests that as polar bears have diverged from brown bears, changes in

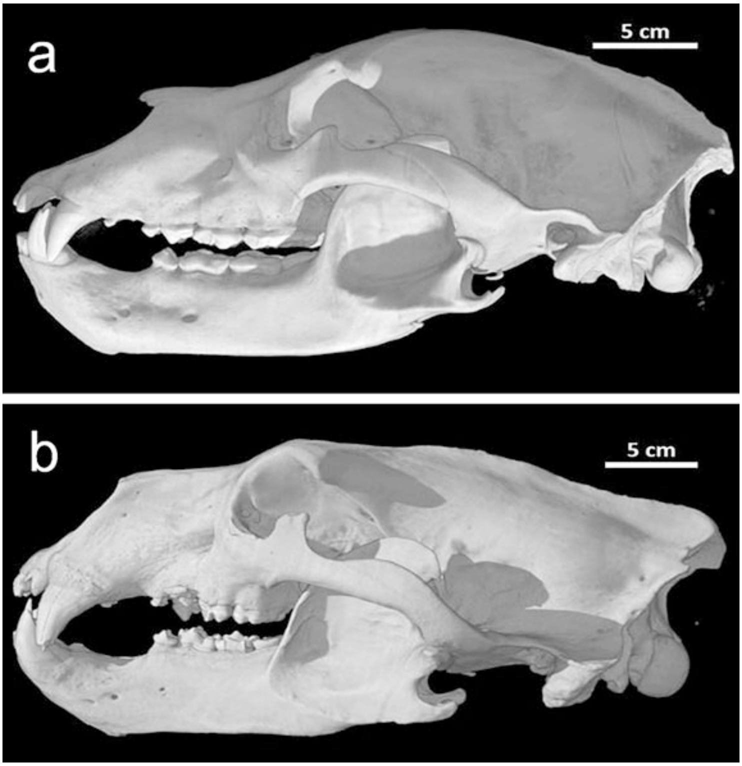

Fig. 12.1 Skulls of (**a**) brown bear (sex unknown; Texas Memorial Museum TMM M-2749), and (**b**) polar bear (bottom; male; Illinois State Museum H 001-05). Images courtesy of Digital Morphology at the University of Texas at Austin

their skull morphology have left them poorly suited for increased masticatory demands, such as chewing vegetation (Slater et al. 2010). Polar bear turbinates, the delicate frameworks of bone in the nasal cavity, are also unique. In comparison to those of black bears (*Ursus americanus*), brown bears, and other caniform terrestrial carnivores, polar bear turbinates have a greater relative surface area associated with olfaction, possibly reflecting selection pressure for detecting widely-dispersed prey on the sea ice (Green et al. 2012).

In some subpopulations, polar bear skull morphology is changing. In the SBS, the width of the zygomatic bones of polar bears sampled during the spring decreased from 1982–2006 for all age and sex classes, except males $\geq$12 years of age (Rode et al. 2010). Interestingly, bears sampled in autumn showed little change during the same period, although zygomatic width increased for females <8 years (Rode et al. 2010). In East Greenland (EG), the condylobasal skull length of male polar bears declined between 1920–1936 and 1999–2010, and the overall shape of the skull changed between 1892–1939 and 1961–2002 (Pertoldi et al. 2009; Sonne et al. 2013). Like body mass and length, skull size is correlated with the availability of sea ice as well factors such as exposure to pollutants (Pertoldi et al. 2009; Rode et al. 2010; Sonne et al. 2013). The effect of these changes on foraging behavior is uncertain.

Dental morphology is similar among extant bear species, unlike the marked differentiation observed in other Carnivoran families, such as Felidae (Christiansen 2008). All members of Ursidae share the dental formula I 3/3, C 1/1, P 4/4, M 2/3, although the number of premolars may vary from 2–4, and sloth bears (*Melursus ursinus*) lose one pair of incisors as adults (Fig. 12.2). The reduced number of premolars creates a diastema between the canines and molars. This characteristic is generally associated with a herbivorous diet even though it is retained in carnivorous polar bears (Figs. 12.1 and 12.2). However, among Ursidae, polar bears exhibit the smallest molar surface area (i.e., occlusal face) other than sloth bears, likely because of the reduced need for mastication because of their diet (Sacco and Van Valkenburgh 2004; Figueirido et al. 2009). Surprisingly, polar bear carnassial teeth are relatively small and not modified for shearing like other hypercarnivores (Sacco and Van Valkenburgh 2004; Figueirido et al. 2009). Polar bears have the largest upper canines of all Ursidae species other than sun bears (*Helarctos malayanus*), although their large canines are proportional to their body mass (Christiansen 2008). Like those of many other mammals, polar bear teeth exhibit cementum annuli (layers of annual growth) which can be counted in a sectioned and stained tooth for aging (Calvert and Ramsay 1998).

Despite their diet of marine mammals, polar bears do not have specialized teeth for capturing and killing prey like some hypercarnivorous species (e.g., tigers, *Panthera tigris*; Christiansen 2008). This is consistent with the poor performance of the polar bear skull in dissipating bite force stress (Slater et al. 2010). A plausible explanation is that specialized dental weaponry is not required to kill most polar bear prey. For example, ringed seals, which are the primary prey of polar bears in much of the Arctic, are: (1) relatively small, especially pups, (2) easily killed without the need for powerful or prolonged bites, and (3) killed with paw swipes to the head in addition to biting (see Chap. 13; Sacco and Van Valkenburgh 2004). Dental pathologies are common among polar bears. A survey of the teeth and mandibles of 317 polar bear skulls collected from 1906–2011 found that (1) 21% had dental fractures, usually of a canine tooth (2) 13% had bone necrosis indicative of periodontitis and (3) 9% exhibited lesions indicative of temporomandibular joint osteoarthritis (Winer et al. 2016). The effect of these pathologies on hunting success and longevity is uncertain.

12.2.3 Axial and Appendicular Skeletal Morphology

The postcranial morphology of polar bears is typical of Ursidae and their plantigrade, quadrupedal mode of terrestrial locomotion (Pagano et al. 2018a). However, the limb bones may have a greater bone density than those in brown bears, which could reduce buoyancy and benefit swimming, similar to other semi-aquatic

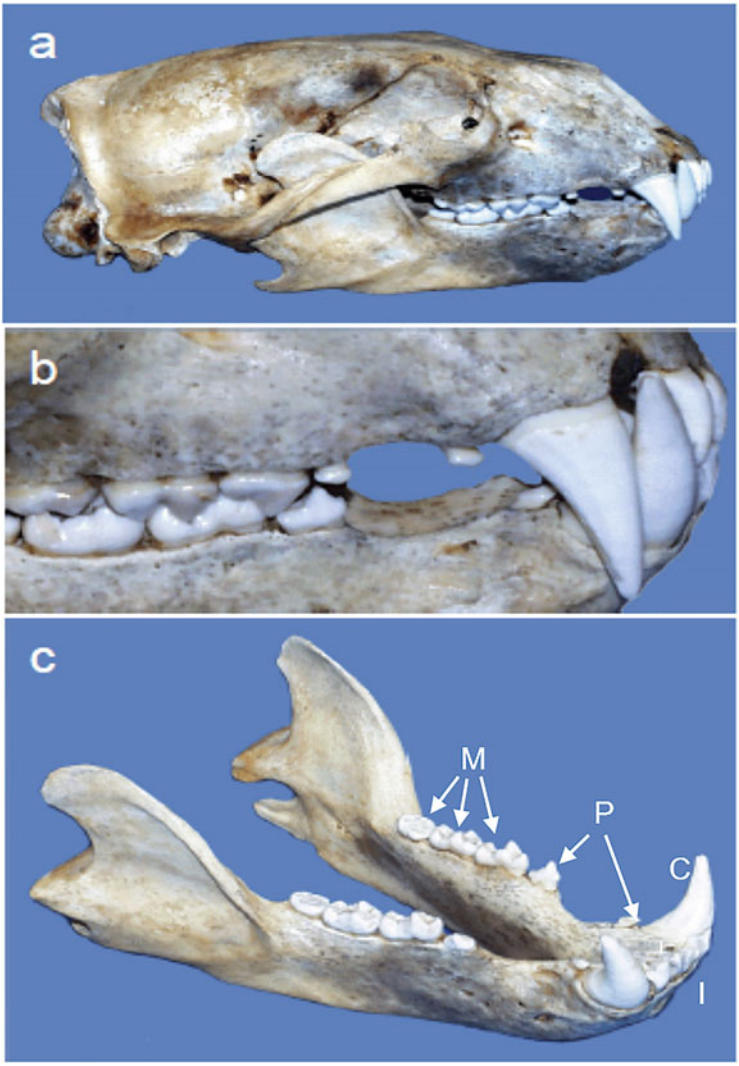

Fig. 12.2 (**a**) Polar bear skull. (**b**) Polar bear dentition showing a diastema in the upper and lower jaws. (**c**) Polar bear mandible showing molars (M), premolars (P; only two are visible on this specimen), canines (C), and incisors (I)

mammals (Wall 1983; Fish and Stein 1991). In comparison to giant pandas (*Ailuropoda melanoleuca*; arboreal as cubs) and sun bears (arboreal as cubs and adults), the tibia in polar bears provides less support for dorsiflexion and supination. These movements are important for tree climbing but are less critical for traversing sea ice (Sasaki et al. 2005). Lastly, pregnant polar bears, which are the only demographic group of this species that reliably hibernate in winter (see Sect. 12.5), appear to increase bone synthesis prior to hibernation (Lennox and Goodship

Fig. 12.3 Ventral view of the foot of a male polar bear captured along the coastline of the Southern Beaufort Sea (SBS), Alaska. For scale, a 10 cm pocketknife is visible in the lower left corner of the image

2008). This may offset bone loss that typically occurs in mammals experiencing months of inactivity. It is unclear whether this increased synthesis occurs in other bear species (McGee-Lawrence et al. 2008).

Polar bear feet are large, possibly for enhanced thrust production during swimming and for distributing body mass over a large area when traversing thin sea ice (Fig. 12.3; Stirling 1999). The footpads are covered with papillae (~1 mm in diameter), creating a rough surface, which enhances traction on sea ice (Manning et al. 1985). The claws are shorter and more curved than those of brown bears, perhaps for grasping prey and for maintaining traction (Amstrup 2003).

12.2.4 Body Composition

Polar bear body composition is highly dynamic. In the SBS, five polar bears sampled at intervals of 8–11 days exhibited mass changes of −10–16%, with changes in lean mass of −7–4% and in fat mass of −9–12% (Pagano et al. 2018b). Nevertheless, their body composition exhibits seasonal trends that reflect their ecology (Arnould and Ramsay 1994; Atkinson and Ramsay 1995; Atkinson et al. 1996; Thiemann et al. 2006; Whiteman et al. 2018). The percent body fat reaches an annual minimum of ~15–25% in spring, before the extensive hunting opportunities of the seal pupping season. Body fat then peaks during summer (~30–40%), after spring hunting has concluded and before the extensive fasting during autumn and winter. The highest percent body fat (~50%) occurs in pregnant females prior to entering winter hibernation (Atkinson and Ramsay 1995; Atkinson et al. 1996).

Polar bears also exhibit variability in the anatomical properties of their lean and fat mass. In spring, their skeletal muscle reaches an annual minimum protein content and maximum water content, consistent with the poor body condition of this season (Whiteman et al. 2017). However, muscle functional characteristics such as fiber type and cross-sectional area do not change seasonally and instead reflect recent activity levels (Whiteman et al. 2017). The lipid content of polar bear adipose tissue is lowest in spring, also correlating with the low overall body condition during this period (Thiemann et al. 2006; McKinney et al. 2014).

Polar bear fat accumulation is primarily subcutaneous, mainly occurring in the rump, although they can possess substantial intra-abdominal and muscular lipid stores (Pond et al. 1992). The subcutaneous adipose tissue of polar bears can be very thick; however, it is not considered blubber as in seals and whales. Indeed, among marine mammals, polar bears and sea otters (*Enhydra lutris*) are notable for their reliance on fur, rather than blubber, for insulation (Liwanag et al. 2012b). Blubber is more homogenous in its anatomical distribution, whereas polar bear subcutaneous fat is accreted in discrete depots with unique anatomical and biochemical properties (Pond et al. 1992; Davis 2019). Also, unlike blubber, in polar bears the distribution of fatty acids (as defined by chain length and saturation) and the thickness of superficial fat are not optimized for insulation (Pond et al. 1992; Grahl-Nielsen et al. 2003; Thiemann et al. 2006).

As with other marine mammals, high concentrations of vitamin A occur in polar bear liver, which can be toxic if consumed (Lewis and Lentfer 1967). Vitamin A precursors are produced by marine algae and can bio-accumulate in apex predators like polar bears (Senoo et al. 2012; Galasso et al. 2017). Accordingly, marine seals feeding at lower trophic levels exhibit lower concentrations of liver vitamin A than polar bears (Lewis and Lentfer 1967). Like nearly all marine mammals (except for the dugong, *Dugong dugon*), polar bears possess multireniculate kidneys (Makita et al. 1998; Williams 2006; Bechshøft et al. 2011a). The origins of this trait remain unclear, although it may be an adaptation for the high dietary salt load, which occurs in the marine environment. Terrestrial bear species also exhibit multireniculate kidneys, possibly indicating a coastal or marine-adapted ancestor for Ursidae (Williams 2006).

12.3 Senses

Vision, audition, and olfaction are important senses for detecting and capturing seals (Owen and Bowles 2011; Green et al. 2012). Polar bear retinas possess the proteins for dichromatic color vision, and behavioral tests of a captive polar bear indicate color perception (Ronald and Lee 1981; Peichl et al. 2005; Levenson et al. 2006). This differs from Cetacea and Pinnipedia, which have monochromatic vision (Davis 2019). Polar bear hearing shows a rapid decline in sensitivity at frequencies of 14–20 kHz, consistent with expectations based on body size (Owen and Bowles 2011). Female polar bears may use odorants to indicate their reproductive status to males during the breeding season. The skin on the bottom of the feet of female polar bears has prominent apocrine glands in association with large hair follicles, and these glands may deposit a scent on the sea ice when they walk (Owen et al. 2015). This would be advantageous because their sea ice habitat lacks stationary, vertical surfaces, such as trees, which are used by other species for scent marking (Owen et al. 2015). Captive male polar bears can distinguish the sex and reproductive status of other individuals based on pedal scent. In addition, both males and females are more interested in pedal scent during the breeding season, demonstrating that scent trails may contribute to seeking and assessing mates (Owen et al. 2015).

12.4 Metabolism

Resting metabolic rate (RMR) is the energy required for basic physiological processes and for heat production to maintain a constant core body temperature. Multiple studies have used respirometry to measure the RMR of captive polar bears at rest, yielding a mean RMR of 0.23 ml O_2 g^{-1} hr^{-1} (0.02 SE) or 1.3 W kg^{-1} for six individuals on a mixed diet of protein and fat (Hurst 1981; Watts et al. 1991; Pagano et al. 2018a). This RMR is approximately twice the predicted value based on body size alone, which is consistent with trends of elevated metabolism for marine mammals and consumers of vertebrate prey (McNab 1988; Williams et al. 2001; Muñoz-Garcia and Williams 2005; Davis 2019). Field metabolic rate (FMR) represents the total energy expenditure by free-ranging individuals exhibiting natural behaviors. Using the doubly-labeled water method, the mean FMR for nine polar bears (mean body mass 176 kg) in the SBS during April was 0.45 ml CO_2 g^{-1} hr^{-1} (0.04 SE). This FMR is equivalent to 52 MJ day^{-1} (assuming an energy equivalence of 26.3 J ml ${CO_2}^{-1}$) or 3.3 W kg^{-1}, which is 2.6-fold greater than the estimated RMR and could be supported by consuming one adult ringed seal every ~11 days (Pagano et al. 2018b).

Locomotion is an important energetic cost for polar bears, and movement rate (km hr^{-1}) is a useful predictor of FMR (Pagano et al. 2018b). Previous studies of polar bears walking on treadmills showed a much higher energetic cost than expected based on body mass, leading to the conclusion that polar bears are inefficient at walking (Best et al. 1981; Best 1982; Hurst et al. 1982). However, these unusually high costs occurred at walking speeds >5.8 km hr.^{-1}, and subsequent studies found that free-ranging polar bears rarely walk that fast (Whiteman et al. 2015). At lower, routine speeds, the cost of terrestrial locomotion is similar to other quadrupeds (Pagano et al. 2018a). Polar bears are powerful, long-distance swimmers and this locomotory cost can contribute to seasonal FMR (Durner et al. 2011; Pagano et al. 2012; Lone et al. 2018). Similar to other semiaquatic mammals (e.g., American mink, *Neovison vison*), the mass-specific energetic cost of swimming for polar bears appears to be higher than for walking, although this difference is not as dramatic as it is in humans (Griffen 2018; Pagano et al. 2019).

For several decades it was thought that all polar bears could facultatively enter "walking hibernation" when food-deprived, including during the summer sea ice melt season (Nelson et al. 1983; Stirling 1999; Dyck et al. 2007; Dyck and Kebreab 2009). This physiological state was hypothesized to include a short-term reduction in metabolism as an energy-conserving adaptation, although this supposition has been revised. In other bears, the decline in metabolic rate during winter hibernation is typically associated with a well-defined decrease in core body temperature (T_b) of 2–5 °C to a new setpoint (Tøien et al. 2011; Friebe et al. 2014). However, during the summer, polar bears in the SBS exhibit a gradual decline in T_b of ~0.7 °C, suggesting a slight and continuous decrease in metabolic rate, which is a typical mammalian response to a long-term reduction in food intake (Whiteman et al. 2015). Similarly, rates of mass loss in polar bears fasting in captivity during summer in WHB (during detention after removal from human conflict) suggest a metabolic rate lower than expected when active but higher than expected during hibernation (Pilfold et al. 2016).

12.5 Thermoregulation

The thermoneutral zone of adult polar bears at rest is not well defined, although it ranges from −30–5 °C (Best 1982). Their upper critical temperature (T_{UC}) is unknown, although a polar bear running on a treadmill at 2.2 m s^{-1} (7.9 km h^{-1}) experienced uncontrolled hyperthermia at a surprisingly low ambient temperature of −25 °C (Best 1982). This suggests that polar bears have a limited capacity to dissipate heat and a low T_{UC}. The lower critical temperature (T_{LC}) of polar bears also is unknown. Similar to many animals, polar bears adjust their resting posture as the ambient temperature declines, curling up to reduce their surface area and retain heat (Øritsland 1970).

The primary defense of polar bears against cold temperatures is their thick fur, which in winter provides a thermal insulation of ~0.8 m^2 °C W^{-1}, which is similar to that in other Arctic mammals such as grey wolves (*Canis lupus*) and caribou (*Rangifer tarandus*) but is less than that of the Arctic fox (*Vulpes lagopus*) and Dall sheep (*Ovis dalli*; Scholander et al. 1950; Hart 1956). Polar bear skin is black, and their fur appears white, although individual hairs are translucent and partially hollow (Wang et al. 2015). Despite speculation that polar bear hair absorbs solar radiation for warmth, this hypothesis is not supported (Koon 1998). The fur is composed of long guard hairs and shorter underhairs, and the morphology of individual hairs is more similar to that of terrestrial mammals, such as Felidae, than aquatic mammals, such as Phocidae (Liwanag et al. 2012a). Foreleg guard hair is substantially longer in males than in females (Derocher et al. 2005). Hair cortisol concentration in polar bears has been used as a proxy for blood cortisol during the period of hair growth, and it has been linked to body condition and annual variation in climate indices (Bechshøft et al. 2011b, 2013; Macbeth et al. 2012). Polar bear fur is replaced annually during a gradual molt, which appears to occur between May and August, although the exact timing and pattern of replacement are unknown (Kolenosky 1987). During this summer molt, the density of the underfur declines substantially, which increases thermal conductance (Frisch et al. 1974).

In water, conductive heat loss through polar bear fur increases by up to 50-fold because the fur does not trap an air layer next to the skin (Scholander et al. 1950; Frisch et al. 1974; Davis 2019). In some marine mammals, such as sea otters, unique hair morphology allows "felting," a process of condensing and pressing fibers together through repeated agitation so that they become tightly interlocked and trap air (Kooyman et al. 1977; Williams et al. 1988). In contrast, air is displaced from polar bear fur upon immersion, and the skin comes into contact with water. The intra-abdominal T_b of polar bears can fall quickly (i.e., $-5\ ^{\circ}\mathrm{C\ hr}^{-1}$) to as low as 22 °C when they swim, suggesting that they reduce blood flow to the skin and some visceral organs to minimize heat loss (Whiteman et al. 2015). Such an adaptation would be similar to the intra-abdominal cooling exhibited by diving king penguins (*Aptenodytes patagonicus*) and emperor penguins (*A. forsteri*; Handrich et al. 1997; Ponganis et al. 2003). Hypothermia in cold water is a particular risk for small polar bears, which likely contributes to the behavior of cubs riding on the back of the mother while she swims (Aars and Plumb 2010; Griffen 2018).

12.6 Reproduction and Hibernation

Reproduction in polar bears is similar to that in other Ursidae (see Chap. 14). From March-June, female polar bears enter estrus, and males exhibit peak testicular function (i.e., spermatogenesis; Spady et al. 2007). The timing of hormonal fluctuations, changes in reproductive tissue morphology, and breeding behavior varies among individuals and subpopulations (Rosing-Asvid et al. 2002; Spady et al. 2007; Gustavson et al. 2015b). During courtship, copulation likely induces ovulation (Stirling et al. 2016). Fertilization is followed by embryonic diapause (i.e., cessation of development) for several months until blastocyst implantation occurs between October- November (Spady et al. 2007). This delayed implantation is similar to that in most Pinnipedia (Pomeroy 2011).

Gestation in polar bears is approximately two months, which is surprisingly short for such a large-bodied mammal, and parturition occurs during hibernation. Among Ursidae, short gestation may be an adaptation to protect the health of the fasting,

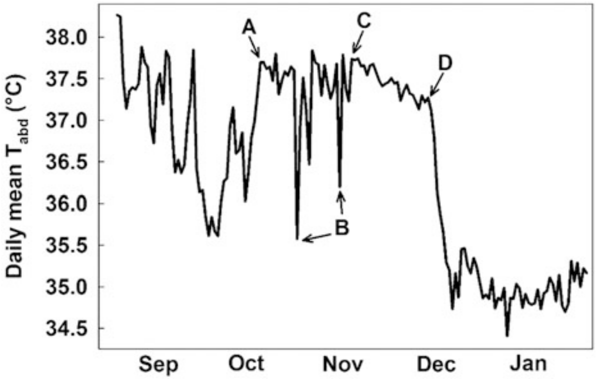

Fig. 12.4 Intra-abdominal body temperature (T_{abd}) of a pregnant polar bear in the Southern Beaufort Sea (SBS) in 2009. During August and September, summer food deprivation likely caused a gradual decline in T_{abd}. (A) An abrupt T_{abd} increase was likely associated with blastocyst implantation, initiating gestation. The bear then began traveling towards its eventual maternal den site, and (B) brief bouts of low T_{abd} likely occurred during swimming events. After entering the den (C), T_{abd} steadily declined, probably to maintain an appropriate temperature gradient for thermoregulation of the rapidly-developing fetus. (D) Parturition likely occurred in early December, immediately followed by a steep decline in T_{abd} to a typical hibernation setpoint. Reproduced from the Supplementary Materials in Whiteman et al. (2015) under the Grant of License to J. P. Whiteman

hibernating mother. Altricial birth favors the depletion of maternal fat stores (during lactation) rather than protein stores (during gestation; Ramsay and Dunbrack 1986). Pregnant females are the only demographic group of polar bears that reliably hibernates in winter, entering maternal dens dug in the snow or earth for up to 200 days (Messier et al. 1994; Ferguson et al. 2000). Other bears (e.g., non-pregnant females with dependent young) may use “shelter dens” for shorter periods (e.g., 50–70 days) during the winter, presumably to avoid inclement weather and poor hunting conditions (Messier et al. 1994; Ferguson et al. 2000). Although the energetics of hibernating polar bears have not been measured directly, respirometry of captive individuals in simulated dens indicates that they reduce their RMR to ~70% based on body mass (Watts and Hansen 1987; Watts et al. 1987). Similar to brown bears, the T_b of female polar bears decreases to a typical hibernation setpoint after parturition (Friebe et al. 2014; Fig. 12.4).

12.7 Feeding and Fasting

Polar bear blood chemistry is an indicator of nutritional status, physiological status, and health (Lee et al. 1977; Tryland et al. 2002; Kirk et al. 2010a; Gabrielsen et al. 2015). Winter is a time of fasting and hibernating for pregnant females and of reduced food intake for other demographic groups. In spring, all polar bears increase their consumption of ringed seals and other marine mammals. In summer and autumn, the nutritional physiology of polar bears is complex. The concept of walking hibernation was thought to include unique nutritional adaptations for fasting in addition to a reduction in metabolic rate (Nelson et al. 1983; Stirling 1999; Dyck et al. 2007; Dyck and Kebreab 2009). To assess these potential adaptations, a study in the SBS examined the nutritional physiology of polar bears during the summer, when this subpopulation temporarily divides into two groups: one on the sea ice and one on shore (Table 12.1; Whiteman et al. 2018). Most variables suggested that during the weeks or months leading up to October, polar bears on the sea ice were in a typical mammalian fast (i.e., they were food-deprived but not catabolizing endogenous protein). This food deprivation likely indicates that the sea ice had retreated to deep water and beyond the distribution of ringed seals on the continental shelf (Harwood and Stirling 1992; Harwood et al. 2012). In contrast, polar bears on shore maintained their lipid and protein stores during the same period by feeding on bowhead whale carcasses left after the human subsistence harvest (Whiteman et al. 2017, 2018).

Although polar bears on the sea ice did not exhibit hibernation-like nutritional adaptations during summer fasting (Table 12.1), they did have low ratios of blood urea-to-creatinine (U:C). This ratio is a key nutritional indicator, with unique relevance for Ursidae (Nelson et al. 1984). Urea is the primary nitrogenous waste product in bears and other mammals. When bears fast during winter hibernation, they stop eating, reduce the catabolism of endogenous protein (i.e., lean tissue), and recycle urea nitrogen in a microbially-mediated process. Accordingly, their blood urea concentration declines substantially (Nelson et al. 1983, 1984; Barboza et al. 1997; Singer 2003; Lohuis et al. 2005; Stenvinkel et al. 2013). This reduces urination and causes creatinine to accumulate (Nelson et al. 1973). As a result, U:C ratios, which are ~20–100 in active, feeding bears, typically fall to ≤10 during hibernation (Nelson et al. 1984; Lohuis et al. 2005; Stenvinkel et al. 2013).

Initial observations of low, hibernation-like U:C ratios in active polar bears during summer prompted the walking hibernation hypothesis (Nelson et al. 1983; Ramsay et al. 1991). However, a presumed key benefit of low U:C ratios (i.e., low protein catabolism) was not extensive in the fasting polar bears on the sea ice in the SBS (Table 12.1; Whiteman et al. 2017, 2018). It is possible that the relatively high metabolic rate and activity level of polar bears during summer, as compared to black and brown bears in winter hibernation, creates such a demand for amino acid catabolism that substantial protein degradation continues, despite recycling of urea nitrogen (Whiteman et al. 2018). Further research using isotope tracers could directly test this hypothesis (Barboza et al. 1997).

Although questions remain regarding the underlying biochemical mechanisms, food deprivation clearly causes U:C ratios to decline in polar bears. In captivity, 13 polar bears had mean U:C ratios of ~30–60 the day after feeding. As the bears fasted, these values declined ~30% after three days and ~50% after seven days (Derocher et al. 1990). Fasting for 36–44 days resulted in a mean U:C ratio of 11–16. Declines in U:C ratios also were observed in free-ranging polar bears that had little or no hunting success over ~10 days of monitoring in the SBS (Pagano et al. 2018b).

Table 12.1 Relative values of blood biochemical variables related to nutrition in polar bears (Whiteman et al. 2018)

		Expected values based on physiological state			Observed values in SBS polar bears in October	
Variable	Description	Feeding	Typical fasting	Hibernation fasting	On sea ice	On shore
NEFA[a,b] (non-esterified fatty acids)	Metabolite released when stored fat is used	Low	High	High	High	Low[c]
ALP[d] (alkaline phosphatase)	Digestive enzyme, falls during fasting	High	Low	Low	Low	High[c]
Albumin[e,f]	Protein, correlates with body protein	High	Low	High	Low	High
Glucose[f,g]	Metabolic fuel	High	Low	High	Low	High[c]
ALT[f] (alanine aminotransferase)	Enzyme for protein catabolism	High	High	Low	High[c]	High[c]
Ghrelin[h,i]	Hormone, stimulates foraging	Low	High	Low	Low[c]	Low[c]
Insulin[g,j]	Hormone, regulates glucose storage	High	Low	High	High[c]	High[c]
Cortisol[k]	Hormone for stress response and use of stored fat	Low	High	High	Low[c]	Low[c]
Creatinine[f,l]	Metabolite, rises when urination declines	Low	Low	High	High	Low
Urea[f,l]	Byproduct of protein catabolism	High	High	Low	Low	High
U:C ratio[f,l] (urea: creatinine)	~10 equated with protein conservation and adaptive fasting	20–100	20–100	10	21 ± 11[m]	10 ± 1[m]

[a] Iqbal and Hussain (2009)
[b] LeBlanc et al. (2001)
[c] Specifically, these values did not differ from individuals sampled during April–May during good hunting conditions on the sea ice
[d] Thompson et al. (1989)
[e] Ballantyne et al. (1973)
[f] Lohuis et al. (2005)
[g] Habold et al. (2005)
[h] Kojima and Kangawa (2010)
[i] Gardi et al. (2011)
[j] Herminghuysen et al. (1995)
[k] Harlow et al. (1990)
[l] Stenvinkel et al. (2013)
[m] Mean ± 95% CI

Overall, a U:C ratio $\leq$ 10–13 indicates that a polar bear has fasted for at least seven days (Cherry et al. 2009; Rode et al. 2018). Such low U:C ratios became increasingly common from the 1980s to early 2000s in polar bears sampled from March–May in the SBS and in the Northern Beaufort Sea (NBS; Cherry et al. 2009; Rode et al. 2018). Most notably in the SBS, the percentage of males exhibiting fasting U:C ratios in the spring rose from 44% (1983–99) to 66% (2000–16), likely related to reduced prey availability and reduced body condition of prey (Cherry et al. 2009; Rode et al. 2018). In the CS, which is adjacent to the SBS and NBS, fewer polar bears exhibited fasting U:C ratios. Furthermore, between the same two time periods (1983–99 and 2000–16), the percentage of females with fasting U:C ratios declined from 53% to 10%. This decrease in spring fasting in the CS likely reflects an increase in spring primary productivity, as this region is one of the most productive areas of the Arctic Ocean (Rode et al. 2018).

Polar bears have a strong preference for dietary fat. Captive polar bears allowed to regulate their own food intake selected for 80–100% blubber and 0–20% meat (Best 1985; Folk et al. 1994). Free-ranging individuals have been observed consuming blubber first from freshly-killed seals and occasionally abandoning carcasses despite substantial meat remaining (Stirling 1974; Stirling and Archibald 1977). This preference appears to allow polar bears to maximize energy intake after a kill, based on the higher energy density of lipids (Stirling and Mcewan 1975; Amstrup 2003).

Likely as a result of high lipid intake, polar bears exhibit high concentrations of total cholesterol ($\geq$300 mg/dL) and triacylglycerol ($\geq$250 mg/dL), which are 25% greater than the levels recommended to humans for avoiding cardiovascular disease (Cleeman et al. 2001). Such high values occur in both captive and free-ranging polar bears (Lee et al. 1977; Kaduce et al. 1981; Folk et al. 1994; Kaduce and Folk 2002; Crissey et al. 2004; Whiteman et al. 2013). However, cardiovascular disease is not a concern for polar bear health, similar to brown bears (Bourne et al. 2010; Arinell et al. 2012; Patyk et al. 2015). Although the protective physiological mechanisms are unknown, polar bears exhibit strong positive selection for genetic traits associated with lipoprotein clearance, vascular morphogenesis, and reduced cardiomyopathy, implying an important reorganization of the cardiovascular system in association with a high-fat diet (Liu et al. 2014). In addition, both wild and captive polar bears have the highest concentration of high-density lipoproteins (HDL) reported for Ursidae (Hissa et al. 1994; Crissey et al. 2004; Frank et al. 2006; Arinell et al. 2012; Whiteman et al. 2013). Their levels of this beneficial cholesterol are 2 to 4-fold higher than the minimum threshold (60 mg/dL^{-1}), which is associated with reduced cardiovascular disease in humans (Cleeman et al. 2001; Schaefer and Asztalos 2007; Tall 2009).

In captive polar bears, seal skin and blubber had a gut transit time of 38 hr compared to 12 hr for herring (Best 1985). The apparent digestibility of seal skin and blubber was 93%, consistent with digestibility of 92–97% for crude protein, 94–100% for crude fat, and 48–57% for crude fiber (Best 1985; Jansen et al. 2003; Dyck and Morin 2011). Fecal microbiota of free-ranging polar bears in the Barents Sea (BS) were dominated by the phylum Firmicutes, especially the genus

Clostridium (Glad et al. 2010). However, captive individuals exhibited more diverse fecal microbiota, likely reflecting differences in diet (Schwab and Ganzle 2011).

12.8 Disease and Immune Function

Morbilliviruses infect polar bears in the wild, with canine distemper virus (CDV) being more common than phocine, dolphin, or porpoise varieties (Garner et al. 2000; Cattet et al. 2004; Kirk et al. 2010b). Antibodies to the parasite *Toxoplasma gondii* have also been detected in polar bears (Kirk et al. 2010b). In the SBS, antibodies for CDV were most common in younger polar bears (79% of individuals sampled; 5–7 years of age), whereas *T. gondii* antibody prevalence did not vary with age (Kirk et al. 2010b). In general, the immune system of polar bears may recognize relatively few pathogens and parasites given the surprisingly low diversity in their major histocompatibility complex (Weber et al. 2013). During summer in the SBS, polar bears on shore exhibit greater immune system activity than individuals on the sea ice, including higher counts of neutrophils and monocytes (Whiteman et al. 2019). These elevated counts may result from exposure to terrestrial pathogens, which polar bears on the sea ice do not encounter. SBS polar bears have different antibody profiles on shore (more *T. gondii*, less *Brucella* spp.) than they do on the sea ice, although the fitness effects of these differences are unclear (Atwood et al. 2017).

In general, most infectious diseases for polar bears are unknown (Fagre et al. 2015). For example, periodic outbreaks of alopecia associated with reduced body condition have been observed in the SBS, but the pathogen, thought to be a virus, has yet to be identified (Bowen et al. 2015). Parasites and diseases represent an important research area for polar bears, especially because these factors were ranked seventh in importance out of 24 potential influences on polar bear population dynamics (Fagre et al. 2015; Atwood et al. 2016).

12.9 Physiological Effects of Environmental Contaminants

Similar to most other marine mammals, polar bears are at risk of accumulating high tissue burdens of pollutants because they feed at a high trophic level, are long-lived, and possess substantial lipid stores, which can absorb lipophilic toxins (Desforges et al. 2016). Despite inhabiting regions of low human population, polar bears are exposed to a variety of pollutants that are transported to the Arctic by wind and ocean currents. Because of prevailing currents, the concentration of contaminants, such as organohalogens or polychlorinated biphenyls (PCBs), in polar bear tissues are generally lowest in subpopulations near Alaska and highest in those near Greenland (Bentzen et al. 2008; Dietz et al. 2015). In addition, some contaminants are less common in terrestrial than marine environments, reducing exposure for individuals using shore habitats (Atwood et al. 2017).

Trends in pollutant exposure vary temporally (Letcher et al. 2018). The composition of contaminants in BS polar bears changed between 1967 and 1993–94, most notably a nine-fold increase in one PCB (Derocher et al. 2003). A class of perfluorochemicals recently declined in East Greenland (EG) polar bears, likely because of reduced industrial production in the United States and Europe (Rigét et al. 2013). Contaminant exposure also can be associated with climate change and sea ice loss. Organohalogen and mercury accumulation is higher for polar bears in food webs that have greater primary productivity from open-water phytoplankton than from benthic organisms or ice-associated algae. Such a shift in production has occurred in some regions after sea ice loss (Cardona-Marek et al. 2009; McKinney et al. 2009; Horton et al. 2009; McKinney et al. 2010). Many of the pollutants that polar bears absorb accumulate in their tissues. Lipophilic organochlorines are stored in adipose tissue and are transferred to cubs during nursing (Polischuk et al. 2002). Contaminants that bind to proteins rather than lipids increase in the blood during fasting, possibly because of the catabolism and recycling of endogenous proteins (Tartu et al. 2017).

Chemical contaminants have varying physiological effects on polar bears. Organochlorines are correlated with reduced immunoglobulin concentrations and reduced production of antibodies to influenza and reovirus (Bernhoft et al. 2000; Lie et al. 2004). In polar bear brain tissue, mercury levels well below the expected threshold for negative effects show a surprising correlation with a marker of potential neurological damage (Basu et al. 2009). There is particular concern over contaminants that disrupt endocrine functions in polar bears. Concentrations of some PCBs positively correlate with blood progesterone and negatively correlate with thyroid hormones, pregnenolone, and androstenedione (Haave et al. 2003; Gabrielsen et al. 2015; Gustavson et al. 2015a). The net effect of chemical contamination at the organismal and population scale is difficult to predict because of the complex ecology of this species. Nevertheless, contaminants may be responsible for pseudohermaphroditism in BS polar bears (Wiig et al. 1998). Studies of model organisms such as rats suggest that contaminant levels in free-ranging polar bears are high enough to hinder reproduction, affect fitness, and influence population vital rates (Dietz et al. 2015, 2018).

12.10 Future Research

Many research questions remain about the organismal biology of polar bears. Despite extended fasting being an inherent part of their annual cycle, it is unclear whether they retain and recycle urea nitrogen as occurs during hibernation in other bear species (Whiteman et al. 2018). Although their preference for dietary fat is well documented, there is only indirect evidence for genetic alterations of lipid metabolism (Liu et al. 2014; Rinker et al. 2019). Pathogens, which may affect fitness, are largely unidentified, and the population-scale effects of contaminants have yet to be conclusively assessed (Fagre et al. 2015). Importantly, polar bears should be studied in the context of environmental change and ongoing sea ice loss. Overall, population modeling indicates that the global abundance of polar bears has a 71% probability of declining >30% during the next ~40 years (Regehr et al. 2016). Physiological responses to environmental change will be crucial for their survival. Our current knowledge indicates the dependence of polar bears on the sea ice environment and the prey that it provides, a connection that links the alteration and loss of this habitat to the fates of individual animals and to the future of the species.

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