

Chapter 16

Polar Bear Behavior in Response to Climate Change



Jon Aars

Abstract Although the Arctic has experienced previous periods of warmer climate, the rate of sea ice loss in recent decades is likely faster than polar bears have ever experienced. The rapidly changing climate means that any response in polar bear behavior is unlikely to be driven by microevolution, but rather it will depend on behavioral plasticity. Fortunately, studies indicate high behavioral plasticity in polar bears despite their marked specialization as a marine predator. Although seals are their primary prey, polar bears feed opportunistically on a variety of marine and terrestrial prey and vegetation. Recently, the greatest change in their feeding behavior has resulted from spending more time on land as seasonal sea ice recedes. Additionally, polar bears will encounter new prey as some temperate species extend their ranges northward. Changes in polar bear movements and habitat associations because of climate change vary among subpopulations. In several areas, the loss of sea ice has altered migration routes, required long-distance swimming between hunting and denning areas, and resulted in some denning areas becoming inaccessible. Because polar bears do not occur in regions without sea ice for a significant part of the year, a diet of seals may not be fully replaceable with alternative terrestrial food, which poses a serious conservation concern.

Keywords Adaptation · Behavior · Climate · Den · Foraging · Habitat · Mating · Microevolution · Plasticity · Polar bear · Sea ice

During the past three decades, climate change has led to an ice-free season that is weeks or months longer than historical periods in several areas occupied by polar bears (Regehr et al. 2016; Stern and Laidre 2016). The Arctic has been warming at a rate about twice the global average and, in addition to the longer ice-free season,

J. Aars (✉)
Fram Centre, Norwegian Polar Institute, Tromsø, Norway
e-mail: jon.aars@npolar.no

This is a U.S. government work and not under copyright protection in the U.S.; foreign copyright protection may apply 2021
R. W. Davis, A. M. Pagano (eds.), *Ethology and Behavioral Ecology of Sea Otters and Polar Bears*, Ethology and Behavioral Ecology of Marine Mammals,
https://doi.org/10.1007/978-3-030-66796-2_16

there has been an increase in habitat fragmentation and a decrease in multiyear sea-ice, factors that affect sea-ice dependent Arctic mammals (Fig. 16.1; Laidre et al. 2015). This rapid change means that any response in behavior is unlikely to be driven by microevolution, but rather it will depend on behavioral plasticity. Fortunately, studies indicate high behavioral plasticity in polar bears (*Ursus maritimus*) despite their marked specialization as a marine predator that depends on sea ice-associated seal species.

16.1 Changes in Feeding Behavior

Polar bears are the most carnivorous bear species and prey on sea ice-associated seals, mainly ringed seals (*Pusa hispida*) (see Chap. 13). However, they are opportunistic and may eat almost anything. More than 80 species of mammals, plants, birds, fish, and invertebrates have been identified in polar bear diets (Derocher 2012). While their diet may include plants and terrestrial prey when on land, they now spend more time ashore, which increases the frequency of terrestrial foraging. This change in diet has implications for how polar bear subpopulations will survive in the future.

Most data on polar bear foraging have relied on indirect methods rather than direct observations. A Canadian Arctic study of more than 1700 live-captured bears used fatty acid analyses to identify prey species for ten polar bear subpopulations (Thiemann et al. 2008). The data show that polar bears exhibit geographic variation in foraging, but relationships between sea ice conditions and prey dynamics are complex. There are considerable differences in foraging among the sexes and age groups, with adult males hunting larger prey, such as walrus (*Odobenus rosmarus*) and bearded seals (*Erignathus barbatus*), compared to younger males and females of all ages (Thiemann et al. 2008). Walruses (and to a lesser degree, bearded seals) are less sea ice-dependent than ringed seals, suggesting that adult males have an advantage over females and younger males as sea ice is reduced. In Svalbard, bearded seals were more important to polar bears than ringed seals in the summer (Derocher et al. 2002). Conversely, bearded seals were of minimal importance in some areas in the spring, and ringed seals were the most important prey based on scat samples from more than 100 bears collected from 2003-04 (Iversen et al. 2013). Two studies in Svalbard showed a significant change in polar bear foraging. One observed that polar bears on the west coast of Spitzbergen, the most western and largest island in the archipelago, increased consumption of bird eggs in summer (Prop et al. 2015). Farther east in Svalbard, the other study also observed that bears now spend more time in areas with colonies of ground-nesting birds (Hamilton et al. 2017). At the same time, bears spent less time hunting ringed seals at glacial fronts in summer, even though these areas are still used by seals (Hamilton et al. 2017). However, the sea ice is now mostly absent in front of glaciers during the summer, meaning bears no longer have a stable platform for hunting seals. Even in spring, many of the glacial fronts have been without sea ice in recent years. In winter, icebergs from

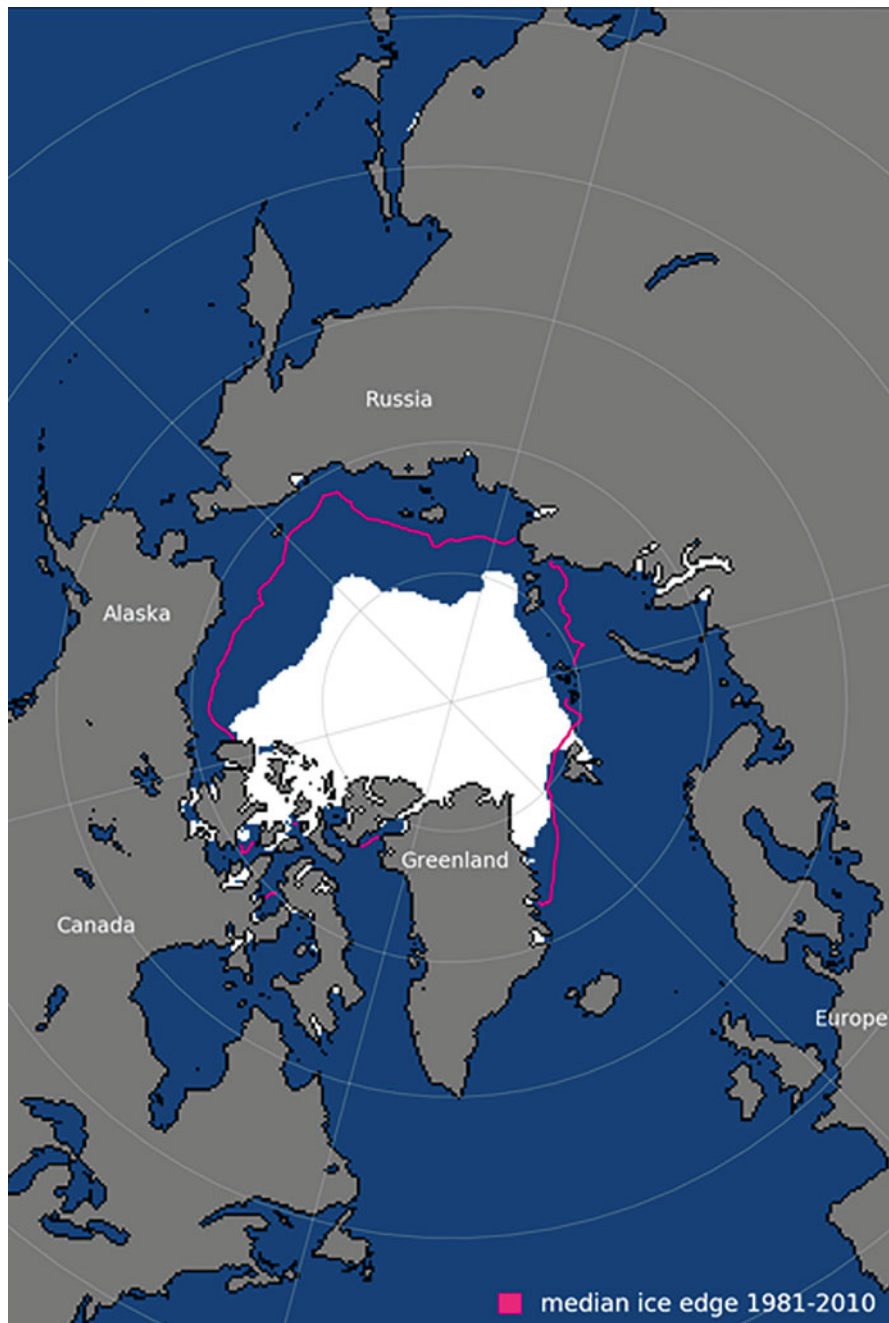


Fig. 16.1 Sea ice cover in September 2019 compared to the median cover from 1981–2010. Image from the National Snow and Ice Data Center, University of Colorado, Boulder

glaciers freeze into the sea ice, causing drifting snow to accumulate. Female ringed seals use these snowdrifts to make their lairs, and female polar bears with cubs hunt seal pups in early spring. In recent years, the sea ice habitat in front of the glaciers has melted by early spring, forcing polar bear mothers to hunt in other areas, potentially traveling farther north to reach the ice edge.

Bowhead whales (*Balaena mysticetus*) are also an important resource for polar bears and may provide food for extended periods when sea ice is scarce (Laidre et al. 2018). In some areas, subsistence whale hunting means carcasses are regularly available, but in other areas, dead whales may wash ashore. Historically, whale carcasses may have been more important when periods of warmer climate led to significant reductions in Arctic sea ice habitat, but fewer whale carcasses will be available in the future because whaling greatly reduced stock sizes (Laidre et al. 2018). In the Beaufort Sea, polar bears frequently feed on bowhead carcasses from subsistence hunting (Amstrup 2003). In good ice years, this resource is important for some bears during the summer, but it will likely increase in importance as the length of the ice-free season increases (see Chap. 13). Bears may change their home range significantly when they learn that whale carcasses are regularly available (Lillie et al. 2018).

While large whales are only a food source as carcasses, polar bears will hunt and kill smaller whales (Amstrup 2003). Both narwhals (*Monodon monoceros*) and beluga whales (*Delphinapterus leucas*) are associated with sea ice, and their abundance may decline as the sea ice declines. Polar bears wait along leads and near small areas of open water for narwhals, which occasionally become trapped in the sea ice. In Svalbard, polar bears killed white-beaked dolphins (*Lagenorhynchus albirostris*), which became trapped in the sea ice during a period of cold spring weather (Fig. 16.2; Aars et al. 2015). These dolphins normally do not occur so far north at that time of the year, and their presence likely resulted from recent climate changes when many species have expanded their range northward. However, it is uncertain whether white-beaked dolphins and other more southerly species will become significant prey for polar bears in the future. Increased open water resulting from climate change likely will reduce the foraging success of polar bears on smaller, sea ice-dependent whales.

In Svalbard, observations of polar bears killing reindeer (*Rangifer tarandus*) were previously rare (Derocher et al. 2000). More recently, reindeer killed and scavenged by polar bears are more common (Aars unpub. obs.). A local hunter in Svalbard observed several kills or remains of kills, and it is likely that a few bears have specialized in hunting reindeer during periods with little sea ice and reduced access to ringed seals (T. Sandal, pers. com.). It is difficult to determine whether polar bears are hunting more reindeer or whether this results from more people observing them. In the future, reindeer may become more common in Svalbard as a warmer climate increases the duration of the growing season. However, it remains to be seen whether reindeer become an important food source for polar bears. Svalbard differs from other areas with large ungulates because competing predators, such as brown bears (*Ursus arctos*) and wolves (*Canis lupus*), are absent.



Fig. 16.2 A male polar bear with a recently killed white-beaked dolphin. There is a small hole in the ice to the left of the dolphin, probably where it surfaced to breathe. Another partially eaten dolphin was found nearby (Aars et al. 2015)

Walrus are less sensitive to sea ice loss than many Arctic marine mammals. Although they are challenging prey to kill because of their large size and defensive behavior, walrus may be an important prey for polar bears in some areas. Polar bears will scavenge dead or debilitated walrus and also prey on calves. On rare occasions, large polar bear males will successfully kill adult walrus. Before being hunted by humans to near extinction, walrus on the west coast of Spitsbergen (Svalbard) may have sustained large numbers of polar bears (Lønø 1970; Kovacs et al. 2014). Hence, walrus may offer an increasingly important food source as sea ice becomes less abundant and bears are stranded on land for longer periods. Polar bears frequently stay close to walrus colonies in the summer, and walrus react to bears, indicating they are a threat (Øren et al. 2018). On Wrangel Island in the eastern Russian Arctic, large aggregations of walrus are important for an increasing number of polar bears on land in summer (Ovsyanikov 2005).

In Western Hudson Bay, polar bears prey on harbor seals (*Phoca vitulina*), which are absent from much of the high Arctic but may move farther north as the climate warms (Thiemann et al. 2008). The most northern population of harbor seals occurs in western Svalbard (Merkel et al. 2013). During the summer, a few polar bears overlap with this population, and some bears ambush the seals from the sea when they haul out onshore. It is likely that predation on harbor seals during the summer has increased in response to an increase in their availability and because polar bears in recent years have not had sea ice in summer from which to hunt ringed seals.

In the summer, polar bears also have been seen catching freshwater fish, such as Arctic char (*Salvelinus alpinus*) and fourhorn sculpin (*Myoxocephalus quadricornis*) (Dyck and Romberg 2007). This has led to a debate about the value of alternative food sources and the adaptability of polar bears in areas with loss of sea ice habitat. However, polar bears catching fish is not a new phenomenon. In Labrador in the summer of 1778, polar bears were observed catching salmon in a river, similar to the behavior of brown bears (Stirling 2011). It is likely that polar bears will depend more on fish in areas of declining sea ice, but some argue that fish alone cannot provide all of the energy they need (Stirling and Derocher 2012).

Polar bears may ingest material that has no nutritional value, although it may contain certain minerals. I once observed a young polar bear during the autumn in Svalbard eating soil while it was recovering from immobilization drugs. Later the same day, I found a large scat from an adult polar bear that was composed solely of claylike soil. A trapper told me that he found several kilos of pebbles in the stomach of a polar bear, which was killed in Svalbard in the 1960s.

Polar bear prey do not need to be large. In Churchill, Canada, in October 2017, I observed a polar bear successfully hunting abundant meadow voles (*Microtus pennsylvanicus*) moving among pieces of wood, kelp, and stones in the littoral zone. If polar bears are on land for long periods, they may behave like brown bears, which are opportunistic carnivores willing to feed on small mammals and birds. When a polar bear's fat reserves are depleted, it likely will feed on any edible plant or animal to avoid starvation.

In winter and spring 2004, intraspecific killing was observed on three occasions, a behavior not seen previously during 24 years of research (Amstrup et al. 2006). Nutritional stress resulting from longer, ice-free seasons could have been the cause. Polar bears also may regard humans as prey and, with bears spending more time on land, the likelihood of aggressive encounters will increase (see Chap. 17).

16.2 Movements and Habitat Use

Loss of sea ice ultimately leads to changes in movements and habitat associations of polar bears. In seasonal ice areas, the amount of time polar bears are stranded on land has increased as the climate has warmed (Amstrup et al. 2008; Stern and Laidre 2016). In Western Hudson Bay, where all polar bears summer on land, the ice-free season increased by three weeks from 1979–2015 (Castro de la Guardia et al. 2017). In Baffin Bay, polar bears exhibited a 70% reduction in summer home ranges and used areas farther north because of a reduction in summer sea ice from 1991–95 and 2009–15 (Laidre et al. 2018).

The Barents Sea has experienced the greatest declines in sea ice of any region in the Arctic (Stern and Laidre 2016). Although polar bears follow the sea ice as it retreats north in summer, they exhibit two habitat preferences (1) an offshore pelagic zone along the ice edge where seals are hunted year-round, especially in the summer and autumn, and (2) a near-shore zone in Svalbard year-round (Mauritzen et al.

2001). Many of the pelagic bears migrate between Svalbard, where females den or where sea ice in winter makes it possible to hunt, and the western Russian Arctic. However, the seasonal ice edge is now located much farther north than it was three decades ago, and this has forced polar bears to hunt farther north (Lone et al. 2018a). In the past, Svalbard was connected to the sea ice year-round. In recent years, open water has separated the archipelago from the ice edge almost annually and in some years well into winter. Although historical data are scarce, polar bears did not swim far to reach the ice edge. In recent years, we have documented bears swimming between Svalbard and the ice edge, which may exceed 100 km and require several days (Lone et al. 2018b). Long swims have been associated with reduced sea ice in other Arctic subpopulations (Pagano et al. 2012; Pilfold et al. 2017). In the Southern Beaufort Sea, long-duration swims by polar bears have been reported, the most extreme of which was almost 700 km over nine days (Durner et al. 2011; Pagano et al. 2012). In 2018, sea ice disappeared entirely in the early summer between Svalbard and Franz Josef Land in the western Russian Arctic. A satellite-collared adult female swam for over a week, interrupted by a 20-h break about halfway. These examples demonstrate the remarkable swimming endurance of polar bears, especially because it is energetically expensive and increases heat loss (see Chap. 12). The estimated energetic cost of swimming is about five-fold greater than that of walking (Griffen 2018).

A few hundred bears reside in Svalbard year-round (near-shore bears). They do not have the same challenges as pelagic bears in moving to denning areas because they usually den close to their summer range. However, with longer ice-free seasons, near-shore bears now spend more time on land and increasingly depend on terrestrial food, which may have a lower energy content. Although pelagic bears expend more energy associated with walking and swimming, their diet of seals potentially provides more energy (Mauritzen et al. 2003; Blanchet et al. 2020). It is difficult to predict which strategy will prove most successful as the loss of sea ice continues. If the distance between the ice edge and Svalbard increases, it is likely that more bears will den in Franz Josef Land, which is closer to the ice edge.

16.3 Denning

In cold-temperate areas with limited food availability in winter, black bears (*Ursus americanus*) and brown bears exhibit obligatory denning. Both male and female polar bears may den for periods of several weeks if weather and prey availability are unfavorable (Amstrup 2003). However, only females giving birth occupy dens for several months (Amstrup 2003). There have been several studies on polar bear denning phenology (i.e., seasonality), mostly based on satellite-collared adult females. Location, ambient temperature, and some indices of activity provide useful indicators of denning events. Denning phenology varies geographically, with den entry mostly from September–November and den emergence from late February–mid-April (see Chap. 14; Amstrup 2003). Cubs are born by early January, but the

timing varies with entry and emergence dates. The duration of time in a den will depend on maturation of the cubs and their ability to follow the female when she leaves the den and synchronization with the ringed seal pupping season. In spring, ringed seal pups are born in subnivean lairs above breathing holes where they remain for several weeks. The altricial pups are easier prey for polar bears than are adult seals. Because female polar bears fast for up to eight months, their fat reserves are low at the end of denning (Atkinson and Ramsay 1995). After emerging from the den, females must find prey to restore fat reserves and provide milk for growing cubs.

It is likely that variation in emergence dates among polar bear subpopulations is partly explained by geographic variation in the occurrence of ringed seal pupping, which indicates the importance of this food source. However, there is considerable variability in the dates of den emergence, indicating the influence of other factors (Hansson and Thomassen 1983). An early decline in sea ice because of a warmer climate could result in earlier ringed seal pupping. As a result, polar bears may enter the den, give birth, and emerge earlier. However, seasonal light levels may limit how much earlier seal pupping and den emergence can occur. In addition, phenological shifts are complicated by what happens before denning. A female must accumulate sufficient fat to fast and produce milk for one to three cubs during the winter.

Changes in the phenology of maternity denning indicate that climate does play a role, but patterns are complex and vary among areas. Polar bears in Baffin Bay from 2009–15 had a mean denning period about one month shorter than in the 1990s, which resulted when females entered dens considerably later (Escajeda et al. 2018). Denning females in the Chukchi Sea, which were in better body condition than females in the Beaufort Sea, emerged from dens later in spring (Rode et al. 2018). Even though sea ice availability would indicate greater food availability, bears did not enter dens later in years with extensive autumn sea ice. However, in the Barents Sea, the start of denning was found to begin later in autumn in years with colder weather (higher Arctic Oscillation index) during the previous spring (Sulich 2019). These females also emerged later if they were older than 10 years. This may result from young females having lost young cubs or having to start hunting earlier if their fat reserves were low in early spring. It also may indicate that bears will shift their denning phenology to earlier in the year as the climate warms and access to seals is further reduced. In Western Hudson Bay, females now emerge from dens several weeks earlier than decades ago (Derocher 2012). In addition, the locations of dens are moving farther north.

In the Southern Beaufort Sea, where most polar bears previously denned in the multiyear ice, they increasingly do so on land as the seasonal sea ice moves farther north (Fischbach et al. 2007; Olson et al. 2017). A reduction in multiyear ice and the greater geographic movement of thinner ice because of sea currents (a den may move hundreds of kilometers from its origin) during the winter may now discourage bears from denning on the sea ice. In Svalbard, dens were common on isolated islands in the eastern archipelago. However, bears can no longer reach Hopen Island (an isolated southern island in the Svalbard archipelago; 76.5° N) because sea ice no longer forms around the island until late in the year (Derocher et al. 2011).

Previously, this island would have had more than 30 dens each year if the sea ice formed by early November. The northern island of Kongsøya, Svalbard (78.9° N) also has experienced a later return of sea ice in recent years, and few if any females now den there. Kongsøya had previously been one of the most important denning areas for polar bears in the Arctic and was protected from hunting in 1939. We do not know how the loss of traditional denning areas will affect the Barents Sea subpopulation. Many pregnant females may find suitable denning areas elsewhere, perhaps in Franz Josef Land in the western Russian Arctic. A genetic study from Svalbard indicated that flexibility regarding denning areas may be large, despite denning philopatry (Zeyl et al. 2010). When possible, polar bears prefer to den near the place of their birth. Although the distance from the ice edge may be within their swimming capability, the energetic cost of swimming long distances (i.e., >100 km) may deplete fat reserves essential for fasting and lactation in the den. In August 2015, my colleagues and I captured two adult females on Kongsøya and instrumented them with GPS satellite collars. There was no sea ice around the island, and both swam about 100 km to reach another island within one week. On Kongsøya, there was nothing to hunt, and the sea ice did not form for several months. Remaining on Kongsøya may have prevented the bears from gaining adequate fat reserves before denning.

In general, the availability of sea ice and food dictates both the distribution of polar bear dens and denning phenology, but these vary geographically depending on the type of habitat. In areas with considerable multiyear sea ice and few open leads, temporary reductions in sea ice may improve the bears' ability to hunt seals (Stirling and Derocher 2012). Flexible denning behavior may be important as the climate warms. For example, it was reported that a female with cubs emerged from a den as early as 8 January (Rode et al. 2018). In Svalbard, a female went into her den as late as 19 January and left with a cub on 1 May. Such plasticity indicates significant flexibility in denning phenology in response to environmental changes.

16.4 Weaning

In most areas, females stay with their cubs for a little over two years (until spring when females mate again). Although this was true for polar bears in Western Hudson Bay in the 1980s, a 3-year reproductive cycle is common in most areas if cubs survive.

16.5 Mating

Polar bears mate in spring, usually from February–May, with variation in timing among subpopulations (Amstrup 2003). Because of delayed implantation, the fertilized egg does not develop until autumn, and altricial cubs are small when born in

mid-winter. Males roam over large areas searching for females, and because there may be two to three-fold more adult males than receptive females without cubs, competition among males is fierce (see Chap. 14). Females may mate with several males successively over several weeks, and males may guard females for longer periods, then search for new females. As with brown bears, within-litter multiple paternity may occur (Zeyl et al. 2009a). A reduction in sea ice may reduce the home range of males, the number of male-female encounters and copulations, and the variance in male reproductive success. Among polar bear subpopulations, the age at first reproduction varies from 4-6 years and probability depends on food availability (Stirling 2011). Differences in movements of females and males in ice-covered areas in spring may result from female hunting behavior, while males optimize the likelihood of encountering females (Laidre et al. 2013). The reduction in sea ice may lead to more isolated stocks and increased levels of inbreeding, which is normally rare around Svalbard (Zeyl et al. 2009b). The reduced mobility of males and females may further isolate subpopulations geographically.

While the mating season normally occurs in the spring, delayed implantation makes some plasticity possible. A highly unpredictable environment means cubs could starve if the female has insufficient fat reserves and is unable to catch prey. However, the female's condition can improve rapidly if food is plentiful (see Chap. 13) and, in such cases, being able to mate in summer rather than waiting until the following spring would increase her expected lifetime reproductive success. In one instance, a mating occurred in late June in Svalbard involving a female that had lost a yearling cub earlier in the spring (Smith and Aars 2015). This female went into a maternity den the following winter. The possibility of mating in the summer may be important if diminished sea ice leads to unpredictable food availability in the spring.

16.6 Conclusions

Polar bears may change their behavior in response to a warmer climate and less sea ice. Most of the change will result from phenotypic plasticity rather than microevolution because the environmental changes are occurring over a few generations. While the ability to swim long distances is important in an increasingly fragmented sea-ice habitat, the energetic cost is large. The ability to maintain fat reserves will be critical during periods of reduced access to seals. Although several studies have shown a negative relationship between polar bear viability and residency on land, the importance of alternative terrestrial food sources is unclear. Because polar bears do not occur in any ice-free areas for a significant part of the year, a diet of seals may not be fully replaceable with alternative terrestrial food, which poses a serious conservation concern.

References

- Aars J, Andersen M, Brenière A, Blanc S (2015) White-beaked dolphins trapped in the ice and eaten by polar bears. *Polar Res* 34:26612
- Amstrup SC (2003) Polar bear, *Ursus maritimus*. In: Feldhamer GA, Thompson BC, Chapman JA (eds) *Wild mammals of North America: biology, management, conservation*. Hopkins University Press, Baltimore, pp 587–610
- Amstrup SC, Stirling I, Smith TS, Perham C, Thiemann GW (2006) Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biol* 29:997–1002
- Amstrup SC, Marcot BG, Douglas DC (2008) A Bayesian network modeling approach to forecasting the 21st century worldwide status of polar bears. *Geophys Monogr Ser* 180:213–268
- Atkinson SN, Ramsay MA (1995) The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). *Funct Ecol* 9:559–567
- Blanchet MA, Aars J, Andersen M, Routti H (2020) Space-use strategy affects energy requirements in Barents Sea polar bears. *Mar Ecol Prog Ser* 639:1–19
- Castro de la Guardia L, Myers PG, Derocher AE, Lunn NJ, Terwisscha van Scheltinga AD (2017) Sea ice cycle in western Hudson Bay, Canada, from a polar bear perspective. *Mar Ecol Prog Ser* 564:225–233
- Derocher AE (2012) *Polar bears: a complete guide to their biology and behavior*. Johns Hopkins University Press, Baltimore, MD
- Derocher AE, Wiig Ø, Bangjord G (2000) Predation of Svalbard reindeer by polar bears. *Polar Biol* 23:675–678
- Derocher A, Wiig Ø, Andersen M (2002) Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biol* 25:448–452
- Derocher AE, Andersen M, Wiig AJ, Hansen E, Biuw M (2011) Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Mar Ecol Prog Ser* 441:273–279
- Durner GM, Whiteman JP, Harlow HJ, Amstrup SC, Regehr EV, Ben-David M (2011) Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. *Polar Biol* 34:975–984
- Dyck MG, Romberg S (2007) Observations of a wild polar bear (*Ursus maritimus*) successfully fishing Arctic charr (*Salvelinus alpinus*) and Fourhorn sculpin (*Myoxocephalus quadricornis*). *Polar Biol* 30:1625–1628
- Escajeda E, Laidre KL, Born EW, Wiig Ø, Atkinson S, Dyck M, Ferguson SH, Lunn NJ (2018) Identifying shifts in maternity den phenology and habitat characteristics of polar bears (*Ursus maritimus*) in Baffin Bay and Kane Basin. *Polar Biol* 41:87–100
- Fischbach AS, Amstrup SC, Douglas DC (2007) Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. *Polar Biol* 30:1395–1405
- Griffen BD (2018) Modeling the metabolic costs of swimming in polar bears (*Ursus maritimus*). *Polar Biol* 41:491–503
- Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen C (2017) An Arctic predator–prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J Anim Ecol* 86:1054–1064
- Hansson R, Thomassen J (1983) Behavior of polar bears with cubs in the denning area. *Int Conf Bear Res Manag* 5:246–254
- Iversen M, Aars J, Haug T, Alsos IG, Lydersen C, Bachmann L, Kovacs KM (2013) The diet of polar bears (*Ursus maritimus*) from Svalbard, Norway, inferred from scat analysis. *Polar Biol* 36:561–571
- Kovacs KM, Aars J, Lydersen C (2014) Walruses recovering after 60+ years of protection in Svalbard, Norway. *Polar Res* 33:26034
- Laidre KL, Born EW, Gurarie E, Wiig Ø, Dietz R, Stern H, PRS B (2013) Females roam while males patrol: divergence in breeding season movements of pack-ice polar bears (*Ursus maritimus*). *Proc R Soc B* 280:20122371

- Laidre K, Stern H, Kovacs KM, Lowry L, Moore SE, Regehr EV, Ferguson SH, Wiig Ø, Boveng P, Angliss RP, Born EW, Litovka D, Quakenbush L, Lydersen C, Vongraven D, Ugarte F (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv Biol* 29:724–737
- Laidre KL, Stirling I, Estes JA, Kochnev A, Roberts J (2018) Historical and potential future importance of large whales as food for polar bears. *Front Ecol Environ* 16:515–524
- Lillie KM, Gese EM, Atwood TC, Sonsthagen SA (2018) Development of on-shore behavior among polar bears (*Ursus maritimus*) in the southern Beaufort Sea: inherited or learned? *Ecol Evol* 8:7790–7799
- Lone K, Kovacs KM, Lydersen C, Fedak M, Andersen M, Lovell P, Aars J (2018a) Aquatic behaviour of polar bears (*Ursus maritimus*) in an increasingly ice-free Arctic. *Sci Rep* 8:9677
- Lone K, Merkel B, Lydersen C, Kovacs KM, Aars J (2018b) Sea ice resource selection models for polar bears in the Barents Sea subpopulation. *Ecography* 41:567–578
- Lønø O (1970) The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. Norsk Polarinstitutt SKRIFTER NR. 149, Oslo, Norway
- Mauritzen M, Derocher AE, Wiig Ø (2001) Space-use strategies of female polar bears in a dynamic sea ice habitat. *Can J Zool* 79:1704–1713
- Mauritzen M, Derocher AE, Pavlova O, Wiig Ø (2003) Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. *Anim Behav* 66:107–113
- Merkel B, Lydersen C, Yoccoz NG, Kovacs KM (2013) The world's northernmost harbour seal population-how many are there? *PLoS One* 8:e67576
- Olson JW, Rode KD, Eggett D, Smith TS, Wilson RR, Durner GM, Fischbach A, Atwood TC, Douglas DC (2017) Collar temperature sensor data reveal long-term patterns in southern Beaufort Sea polar bear den distribution on pack ice and land. *Mar Ecol Prog Ser* 564:211–224
- Øren K, Kovacs KM, Yoccoz NG, Lydersen C (2018) Assessing site-use and sources of disturbance at walrus haul-outs using monitoring cameras. *Polar Biol* 41:1737–1750
- Ovsyanikov NG (2005) Behavior of polar bear in coastal congregations. *Zool Zhurnal* 84:94–103
- Pagano AM, Durner GM, Amstrup SC, Simac KS, York GS (2012) Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water. *Can J Zool* 90:663–676
- Pilfold NW, McCall A, Derocher AE, Lunn NJ, Richardson E (2017) Migratory response of polar bears to sea ice loss: to swim or not to swim. *Ecography* 40:189–199
- Prop J, Aars J, Bårdsen BJ, Hanssen SA, Bech C, Bourgeon S, de Fouw J, Gabrielsen GW, Lang J, Noreen E, Oudman T, Sittler B, Stempniewicz L, Tombre I, Wolters E, Moe B (2015) Climate change and the increasing impact of polar bears on bird populations. *Front Ecol Evol* 3:33
- Regehr EV, Laidre KL, Akcakaya HR, Amstrup SC, Atwood TC, Lunn NJ, Obbard M, Stern H, Thiemann GW, Wiig Ø (2016) Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. *Biol Lett* 12:20160556
- Rode KD, Olson J, Eggett D, Douglas DC, Durner G, Atwood TC, Regehr EV, Wilson RR, Smith T, St. Martin M (2018) Den phenology and reproductive success of polar bears in a changing climate. *J Mammal* 99:16–26
- Smith TG, Aars J (2015) Polar bears (*Ursus maritimus*) mating during late June on the pack ice of northern Svalbard, Norway. *Polar Res* 34:25786
- Stern HL, Laidre KL (2016) Sea-ice indicators of polar bear habitat. *Cryosphere* 10:2027–2041
- Stirling I (2011) Polar bears: the natural history of a threatened species. Fitzhenry & Whiteside Ltd., Markham, ON
- Stirling I, Derocher AE (2012) Effects of climate warming on polar bears: a review of the evidence. *Glob Chang Biol* 18:2694–2706
- Sulich JM (2019) Denning phenology of polar bears (*Ursus maritimus*) in the Barents Sea population. University of Tromsø, Norway

- Thiemann GW, Iverson SJ, Stirling I (2008) Polar bear diets and arctic marine food webs: insights from fatty acid analysis. *Ecol Monogr* 78:591–613
- Zeyl E, Aars J, Ehrich D, Bachmann L, Wiig Ø (2009a) The mating system of polar bears: a genetic approach. *Can J Zool* 87:1195–1209
- Zeyl E, Aars J, Ehrich D, Wiig Ø (2009b) Families in space: relatedness in the Barents Sea population of polar bears (*Ursus maritimus*). *Mol Ecol* 18:735–749
- Zeyl E, Ehrich D, Aars J, Bachmann L, Wiig Ø (2010) Denning-area fidelity and mitochondrial DNA diversity of female polar bears (*Ursus maritimus*) in the Barents sea. *Can J Zool* 88:1139–1148