# **Chapter 24 Implications of Rapid Environmental Change for Polar Bear Behavior and Sociality**

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**Abstract** Historically, the Arctic sea ice has functioned as a structural barrier that has limited the nature and extent of interactions between humans and polar bears (*Ursus maritimus*). However, declining sea ice extent, brought about by global climate change, is increasing the potential for human-polar bear interactions. Loss of sea ice habitat is driving changes to both human and polar bear behavior—it is facilitating increases in human activities (e.g., offshore oil and gas exploration and extraction, trans-Arctic shipping, recreation), while also causing the displacement of bears from preferred foraging habitat (i.e., sea ice over biologically productive shallow) to land in some portions of their range. The end result of these changes is that polar bears are spending greater amounts of time in close proximity to people. Coexistence between humans and polar bears will require imposing mechanisms to manage further development, as well as mitigation strategies that reduce the burden to local communities.

# 24.1 Introduction

The capacity for environmental change to influence human and wildlife behaviors is nothing new, neither as a theoretical construct nor an empirical reality. The resource heterogeneities and uncertainties arising from changing environmental conditions, in some cases mediated by human activities, have acted as significant stimuli throughout history for behavioral and social change. In some instances, humans and wildlife have responded similarly to environmental change. For example, both have relied on a variety of migration strategies to cope with the seasonality of precipitation patterns, primary productivity, and long-term drought (e.g., Leimgruber et al. 2001; Gereta et al. 2004; Turney and Brown 2007). In other cases, the responses of

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human and wildlife to environmental change have diverged. For instance, in parts of Central and South America, the expansion of transportation infrastructure into previously inaccessible areas has led to deforestation and eventual conversion of land to agricultural practices which, in turn, has greatly decreased the diversity of local floral and faunal communities (Brooks et al. 2002; Mosandl et al. 2008). These examples demonstrate ways in which human and wildlife behaviors and coexistence have been shaped by interactions with the environment and helped biologists identify the relationship between disturbances and patterns of response within communities.

In recent years, biologists have identified key life-history and behavioral traits that influence how species respond to environmental changes, such as habitat fragmentation and loss. Life-history traits, such as body size, govern perceptual ability (e.g., ability to perceive landscape heterogeneity) and determine the spatial scale over which organisms access various resources (e.g., prey, refugia, mates; Wiens 1989). Behavioral traits are usually consistent among populations of a species, are often easier to assess than population demographic variables, and are associated with various environmental variables of interest. Behavioral traits, like plasticity, determine the breadth of a species repertoire for responding to environmental cues, including stressors (Sih 2013). Collectively, these sorts of traits help determine the sensitivity of species to environmental change. As a logical corollary, identifying such traits may allow for greater insight into species responses to rapid environmental changes, like those brought about by a changing climate.

Life-history traits of polar bears (*Ursus maritimus*) are well documented. Polar bears are solitary apex predators that range over vast expanses of sea ice, specialize in preying on ice seals (primarily ringed (*Pusa hispida*) and bearded (*Erignathus barba-tus*) seals), are long-lived, and are characterized by long generation times and interbirth intervals and extended care of dependent young (e.g., Amstrup 2003). By contrast, behavioral traits of polar bears are less well documented. The intent of this chapter is not to provide an extensive review of polar bear behavior, but to provide an overview of how human activities in the Arctic are likely to change behavioral traits that may influence polar bear sensitivity and, possibly, resilience to increasing human activities.

#### 24.2 A Brief Primer on Polar Bear Sociality

Polar bears are non-territorial, ranging over large areas, and males tend to have larger home ranges than females (Amstrup et al. 2001; Laidre et al. 2013). Like most large carnivores, they have a relatively flexible social system that can vary seasonally and geographically. For example, while on the sea ice, males and females are mostly solitary except for the breeding season (April to May), when males adjust their spatial behavior to minimize encounters with other males and maximize encounters with females in estrus (Laidre et al. 2013). Females with dependent young tend to segregate from adult males while raising cubs, and the family group will remain together for approximately 2.5 years, with separation occurring when the adult female breeds again. In subpopulations where land use occurs during summer, bears have been observed aggregating into loose groups. For example, in

western Hudson Bay (WHB), polar bears on land in summer will spatially segregate based on age and sex (Lunn and Stirling 1985; Derocher and Stirling 1990). Males generally remain closer to the coast and will sometimes form small "bachelor groups" of  $\geq 2$  individuals and engage in bouts of play (e.g., sparring; Latour 1981). Conversely, family groups and pregnant females will typically move further inland from the coast to be closer to denning areas (Lunn and Stirling 1985).

Similar to grizzly bears (*Ursus arctos*), polar bears have been observed to be fairly tolerant of each other around food resources. Near Churchill, Manitoba, Canada (WHB subpopulation), polar bears routinely visited local garbage dumps prior to their closure in 2005 (Towns et al. 2009), and while females with cubs could be intolerant of other bears, interactions between sex and age classes were generally nonaggressive (Lunn 1986). In Kaktovik, Alaska, USA (southern Beaufort Sea subpopulation [SB]), large numbers of polar bears congregate near a site ("bone pile") where the unused remains of subsistence-harvested bowhead whales (*Balaena mysticetus*) are dumped (Miller et al. 2006; Atwood et al. 2015). In general, incidents of interspecific strife appear to be rare at or near the bone pile, and mixed family groups often rest in close proximity to each other (Miller et al. 2015; Fig. 24.1).

Polar bear social behavior is more varied and nuanced than described above, but knowledge of the full scope is limited by the challenges associated with being able to routinely observe behavior. Key behaviors such as interspecific interactions and spatial aggregations (grouping together) are readily detectable and are sensitive to



**Fig. 24.1** Polar bear family groups resting on a bluff near the bowhead whale bone pile adjacent to the community of Kaktovik, Alaska, USA, September 2015. Family groups often temporally partition use of the bone pile to avoid adult males and aggression between family groups is rare. *Image credit: S.W. Breck* 

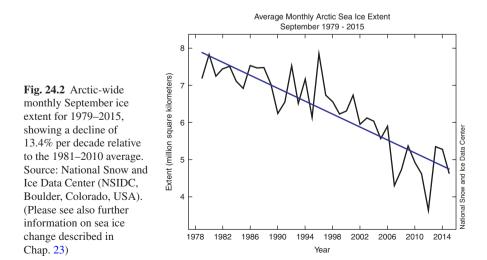
changes in environmental conditions and the availability/accessibility of prey. Derocher and Stirling (1990) posited that aggregating behavior (including the social behavior reported by Latour [1981]) in male polar bears from the WHB subpopulation may function to promote familiarity and thereby reduce the intensity of competition when individuals encounter each other on the sea ice. If correct, and applicable to other regions of the Arctic, aggregating behavior may help attenuate the potential for interspecific strife as climate-mediated accessibility of prey declines over time.

## 24.3 Stressors Likely to Induce Changes in Bear Behavior

#### 24.3.1 Loss of Sea Ice Habitat

Polar regions are experiencing the most acute effects of climate change. Observations over the past 50 years show a pronounced decline in Arctic sea ice extent throughout the year, with the most prominent retreat in summer (Fig. 24.2; Serreze et al. 2007; Comiso 2012). Arctic-wide, the duration of the open-water season (i.e., the period of time between the breakup of sea ice in summer and freeze-up in fall) has increased at a rate of approximately 5 days/decade since 1979 (Stroeve et al. 2014), and some analysts have suggested that the Arctic may be ice-free (i.e., <1 million km<sup>2</sup> of sea ice) in September by 2030 or possibly earlier (Wang and Overland 2009; Overland and Wang 2013). Because of the phenology of sea ice (i.e., timing of annual formation and breakup), the duration of the open-water period is typically greatest for biologically productive (i.e., shallow) waters.

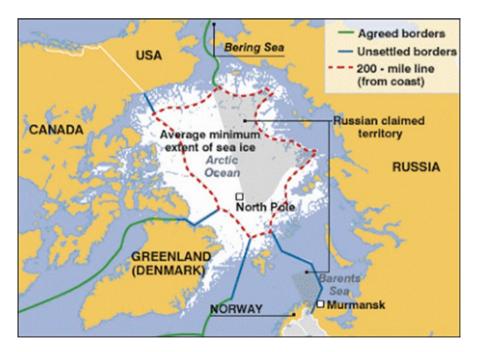
Loss of sea ice over biologically productive waters represents a loss of habitat for polar bears (see Chap. 23 for a full discussion of polar bear-habitat relationships). Durner et al. (2009) used general circulation models (GCMs), and polar bear habitat-use data to project that mean summer optimal habitat within the Polar Basin



(approximately 50% of the most northerly portion of polar bear range) could decrease by 68% by the end of the twenty-first century. Changes to sea ice phenology and habitat quality and distribution have influenced subpopulation vital rates (see Chap. 6.1) and are predicted to also influence subpopulation connectivity and the degree of genetic isolation. The latter are cause for concern given their potential to ultimately influence range-wide population viability.

# 24.3.2 Industrialization

The melting of Arctic sea ice will effectively unlock the Arctic Ocean, leaving it increasingly open to expanding human infrastructure and activities. Arguably, the human activity that generates the greatest concern for the polar bear is resource extraction, which is largely facilitated by increased maritime access. By midcentury, projections of oceanic shipping activity suggest that the five polar bear range state nations will gain increased maritime access to their currently designated exclusive economic zones (i.e., the region for each maritime nation that extends 370 nautical kilometers from the coast; Fig. 24.3), with the greatest increase in access



**Fig. 24.3** A map of the exclusive economic zones (EEZ) of coastal Arctic countries. All countries are entitled to claim an EEZ extending up to 200 miles (*red dotted line*) (370 nautical km) from their coast. The "agreed borders" line delineates the border between each countries claimed EEZ. Where a maritime boundary has yet to be agreed, a line ("unsettled borders") equidistant between the countries is shown. *Source: http://www1.american.edu/ted/ICE/lomonosoy.html* 

occurring for Greenland (28% increase), followed by Canada (19%), Russia (16%), the USA (5%), and Norway (1%) (Stephenson et al. 2011). In turn, increased transiting of Arctic waters will make accessing and transporting the substantive untapped reserves of oil and gas more cost efficient. Projections suggest that the offshore region may contain up to 13% of the global mean estimate of undiscovered oil and up to 30% of the global mean estimate of undiscovered gas (Gautier et al. 2009), which provides a substantial economic incentive for Arctic nations to invest in infrastructure (roads, ports, security) to support industrialization.

Increased maritime access and the likely presence of enormous oil and gas reserves will spur the development of increased infrastructure and human activities in the Arctic, and the impacts of this will be greatest along the coastal and nearshore regions, areas that include valuable foraging (nearshore sea ice) and refugia (coastal lands) habitats for polar bears (Durner et al. 2009; Atwood et al. 2016a, b). In the USA, oil and gas development has largely been restricted to the coastal plain of Alaska's North Slope since 1977 (though nearshore extraction occurs from four artificial islands within 9 km of the coast; Fig. 24.4). However, additional offshore development plans are in place that would greatly expand the existing industrial footprint. For example, the Chukchi Sea Planning Area (CSPA) for offshore oil and



**Fig. 24.4** Aerial view of an oil rig and infrastructure located in Prudhoe Bay, southern Beaufort Sea, Alaska. The oil rig is on an artificial island located approximately 8 km from the coast. A pipeline (right side of figure) runs from the rig to the mainland. *Image credit: US Geological Survey* 

gas development lies approximately 50 km off the coast of northwestern Alaska. There are 487 active leases in the CSPA that cover an area of 225,000 km<sup>2</sup> (Bureau of Ocean Energy Management 2011), and seven exploration wells have been drilled since the early 1990s, with the most recent effort concluding in 2015. Recent analyses indicate that the CSPA may include between 15 and 50% of the total high-value sea ice habitat for the Chukchi Sea (CS) subpopulation of polar bears, depending on the season (Wilson et al. 2014).

In the adjacent southern Beaufort Sea Planning Area (BSPA), there are 183 active leases that cover an area of approximately 4000 km<sup>2</sup>, with production occurring at three sites (Bureau of Ocean Energy Management 2011). Anticipated activities (within the next 10 years) for both planning areas include exploration—with seismic and ancillary surveys when sea ice is present—and eventual extraction (Bureau of Ocean Energy Management 2011). In other areas of the Arctic, there are also plans to conduct exploration and extraction activities (Harsem et al. 2011). Depending on the types of activities conducted, infrastructure could include icebreakers, drillships, multiple support vessels (e.g., for oil storage, spill response), and steel drilling caissons (platforms) as well as tugboat support. Accordingly, these activities could result in fragmentation of sea ice from icebreakers, noise disturbances, and the unintentional release of oil and industrial solvents/chemicals (Johnson et al. 2005; Amstrup et al. 2006; Moore et al. 2012).

To recapitulate, the primary threat to the long-term persistence of polar bears is climate-mediated loss of sea ice habitat (Amstrup et al. 2008; Atwood et al. 2016a); many of the other threats they face, like expanding human activities, are possible mainly because of the changing climate. Below, I discuss how loss of sea ice habitat and increasing anthropogenic activities are likely to drive changes in polar bear social structure and behavior.

## 24.4 Potential Changes in Social Structure and Behavior

#### 24.4.1 Disruption of Gene Flow Between Subpopulations

Movement of individual polar bears between subpopulations has been clearly evident (Taylor et al. 2001; Mauritzen et al. 2002; Amstrup et al. 2004; Crompton et al. 2008) and led some to conclude that polar bears were panmictic (i.e., no mating restrictions throughout the entire range) and thus a single evolutionary unit (Paetkau et al. 1999). However, a recent circumpolar analysis of genetic structure and gene flow dynamics found that the 19 subpopulations studied clustered into four intermediate-scale units that corresponded to current ecological and oceanographic factors (e.g., patterns and timing of sea ice formation and melt, the convergence and divergence of ice from shore, predominant patterns of ice movement; Peacock et al. 2015). Additionally, this same work detected evidence of directional gene flow along a low-to-high latitudinal gradient for a subset of these clusters, which was considered to be generally consistent with a hypothesis of portions of the high Arctic serving as a refugium for polar bears as loss of sea ice habitat continues.

The concern is that continued reductions in the availability and connectivity of sea ice habitat will result in transient refugia and will trigger meta-population dynamics (Peacock et al. 2015) characterized by differential productivity and variable viability of groups of subpopulations. The mainland-island meta-population model, which involves the presence of suitable habitat patches located within dispersal distance from a large habitat patch that supports a permanent population of the species (Hanski and Simberloff 1997), fits polar bear dynamics that are likely to occur if loss of sea ice habitat continues. However, this model requires (1) densitydependent dispersal from mainland (source or refugia) subpopulations to island (sink) subpopulations and (2) enough habitat stability within sink subpopulations to allow year-round residency. The assumption of density-dependent dispersal rests on the notion that carrying capacity in refugia subpopulations is high enough to trigger density-dependent responses, which is not always the case (Betini et al. 2015). Also, while polar bears display high levels of vagility (i.e., ability to move over large areas), there is limited information available to gauge whether changing sea ice conditions may be impacting dispersal ability and frequency. For example, documentation of increased frequencies of long-distance swims (Pagano et al. 2012; Pilfold et al. 2016) suggests that bears are capable of traversing dispersal-like distances through water, but it is unknown if the increase in swimming behavior has compensated for decreased capacity to make long-distance movement over sea ice through loss of navigable ice. Finally, the assumption that there will be sufficient habitat to accommodate the year-round presence of individuals in sink subpopulations is tenuous (see Chap. 23). Projections of future sea ice extent generally show contraction of ice toward the pole, rather than fragmentation dynamics that create "islands" of sea ice habitat in an open-water matrix (IPCC 2014). Given the above, the more likely scenario for circumpolar social structure of polar bears is a coalescence around the Canadian Archipelago (projected to retain year-round sea ice the longest), with some subpopulations seasonally separated during the open-water period due to geographical features and transient use of a wider region of the Arctic during winter when sea ice is at its maximum extent.

#### 24.4.2 Potential Impacts on Denning Behavior

A growing body of evidence indicates that polar bear denning behavior may be compromised by the continued loss of sea ice habitat. In most subpopulations, polar bears establish maternity dens either on land or landfast ice (Ramsay and Stirling 1990; Durner et al. 2003) and typically enter these dens by early November, after sea ice refreezes, providing a connective link between the pack ice and land. However, the increasing duration of the open-water period, and the protracted loss of connectivity between pack ice and land, may impede the ability of bears that mostly reside on sea ice year-round to safely access terrestrial denning habitat (Derocher et al. 2004) (bears in subpopulations that display a seasonal ice life history are onshore prior to denning on land and thus do not rely on connectivity of sea

ice for accessing denning habitat). In the subpopulations of the Polar Basin (northern Beaufort Sea, SB, CS, Laptev Sea, and Kara Sea), the mean date of freeze-up has retreated at a rate approaching 13 days/decade since 1979 (Stroeve et al. 2014). If the pace of retreating freeze-up is maintained, connectivity between pack ice and terrestrial denning habitat could eventually be lost for some subpopulations by the middle of the century, if not sooner (Derocher et al. 2004; Stirling and Derocher 2012).

There does appear to be some capacity for plasticity in polar bear denning behavior. For example, in the SB, denning historically occurred mainly on the sea ice (Lentfer and Hensel 1980; Amstrup and Gardner 1994). However, between 1985 and 2005, a gradual shift in behavior occurred, marked by an increasing frequency of land-based dens such that by 2005, a majority of dens (67%) were located on land (Fischbach et al. 2007). This change in denning behavior occurred alongside declines in multi-year ice which could have affected sea ice stability for denning (Fischbach et al. 2007). The change also occurred concurrent with a greater frequency of long-distance swim events and increasing land use (Pagano et al. 2012; Atwood et al. 2016b), both of which may represent attempts by bears to cope with the increasing open-water period while maintaining access to denning habitat. Polar bear subpopulations that generally remain with the sea ice prior to moving to terrestrial habitats for denning are likely to face growing challenges of accessing land due to the lengthening open-water period (Bergen et al. 2007). It remains unknown whether polar bears have the capacity to shift from terrestrial denning back to a sea ice substrate. There may be a threshold for sea ice retreat, in which greater distances of pack ice from shore preclude bears from safely accessing land, and they choose, instead, to den on sea ice. However, that choice will not be feasible where inadequate pack ice is present.

## 24.4.3 Changes in Spatial Behavior

As mentioned above, in some subpopulations, bears are displaying divergent behavioral strategies for coping with the loss of sea ice habitat, while in others changing sea ice phenology is altering the timing of seasonal migratory movements. In the SB and CS subpopulations, polar bears have mostly remained on the sea ice yearround (with the exception of denning on land). However, over the last few decades, the protracted absence of sea ice from the continental shelf has driven growing proportions of the subpopulations to choose to summer on land rather than remain with the retreating sea ice. For example, in the SB, the proportion of radio-collared female bears on land between August and October increased from approximately 10% to 35% between historical (pre-2000) and contemporary periods (post-2000) (Atwood et al. 2016b), in the CS the proportion of radio-collared female bears on land increased from 20% (1986–1995) to 39% (2008–2013) (Rode et al. 2015). For both subpopulations, the average length of stay on land increased by approximately 30 days and was influenced by the lengthening open-water period. In WHB, where polar bears have historically retreated to land after sea ice melts completely in summer, changes in sea ice phenology have caused bears to adjust the timing of migration from sea ice to land and back. Cherry et al. (2013) examined the timing of arrival of polar bears onshore and departure back to see ice over two time periods, 1991–1997 and 2004–2009, and found the timing of migration showed trends of earlier arrival onshore in summer and later departure back to sea ice in fall, which closely tracked changes in the timing of sea ice breakup in spring and freeze-up in fall.

Changes to sea ice phenology and sea ice habitat connectivity is also believed to be responsible for the increased frequency of long-distance swims by polar bears, some of which are associated with seasonal migration from sea ice to land. In the SB and CS, Pagano et al. (2012) identified 50 long-distance swims (i.e., >50 km) by 20 bears over 6 years (2004–2009). Swim durations ranged from 1 to 10 days, distances ranged from 54 km to 688 km, and the frequency of swim events increased over time (Pagano et al. 2012). Pilfold et al. (2016) observed similar behavior in the Beaufort Sea and Hudson Bay from 2007 to 2012: swim duration ranged from 1 to 9 days, and distances ranged from 51 km to 404 km. In both studies, the majority of swims were associated with seasonal migrations between pack ice and land. Interestingly, Pilfold et al. (2016) found that the frequency of swims was similar for lone adult females and subadults, but lower for adult females with dependent young. This suggests that risk-averse individuals, such as adult females with cubs, may be less likely to undertake a long-distance swim given the energetic consequences and risk to cub survival. Indeed, Durner et al. (2011) describe an instance in which an adult female with a yearling cub made a 687-km swim shortly after being radiocollared. When the adult female was recaptured approximately 2 months later, she had lost 22% of her body mass and the yearling cub (Durner et al. 2011). These results support the hypothesis that long-distance swimming by polar bears is likely to occur more frequently as sea ice conditions change due to climate warming and represent an energetically costly and potentially dangerous mode of transiting fragmented habitat.

#### 24.4.4 Changes to Foraging Behavior

Sea ice loss is increasingly limiting spring and summer hunting opportunities for polar bears (Stirling and Derocher 2012), thereby reducing energy stores available to maintain body condition during the coincident period of general food deprivation (Rode et al. 2010). One way in which bears may cope with declining foraging opportunities, and extended food deprivation, is to limit energy expenditure through reduced activity. For example, Whiteman et al. (2015) found that bears in the Beaufort Sea reduced levels of activity during the open-water season, regardless of whether they were on land or the retreating pack ice. This behavior could represent an attempt to reduce the energetic cost of continued searching for prey by increasing the amount of time spent inactive/resting until prey or other food resources become more accessible.

There is growing consensus that, in summer, polar bears that remain on the retreating pack ice are likely to have limited opportunities to encounter prey (Derocher et al. 2004; Stirling and Derocher 2012; Whiteman et al. 2015). Alternatively, polar bears that spend the summer on land may have greater opportunity to forage on a variety of food items, but the energetic benefit may not be sufficient to prevent declines in body condition in most cases (Rode et al. 2015). For example, in the Hudson Bay region, small numbers of polar bears have been documented consuming terrestrial foods (e.g., Russell 1975; Lunn and Stirling 1985; Ramsay and Hobson 1991; Rockwell and Gormezano 2009; Smith et al. 2010; Iversen et al. 2013), yet body condition and survival have generally declined (Stirling et al. 1999; Regehr et al. 2007). By contrast, polar bears from the SB that summer on land are able to scavenge on human-provisioned bowhead whale (Balaena mysticetus) remains (Atwood et al. 2016b; Fig. 24.5), and there is some evidence to suggest that these bears are in better condition than individuals that summer on the sea ice (US Geological Survey, unpublished data). However, it is important to note that a relatively small proportion (approximately 18%; Atwood et al. 2016b) of the SB subpopulation comes ashore during summer, so there is often limited demand for abundant bowhead whale remains. These findings corroborate the notion that the energy obtained from feeding on most terrestrial-based foods (i.e., protein- and carbohydrate-rich foods) is likely insufficient to offset daily energy expended. If polar bears eventually are forced to spend  $\geq 5$  months on land, it is unlikely that they will



Fig. 24.5 Polar bear family group (mother and cubs) at the bowhead whale "bone pile" in Kaktovik, Alaska, 2009. *Image credit: US Geological Survey* 

be able to adjust their feeding behavior in a way sufficient enough to stave off declines in body mass (e.g., Molnár et al. 2014; Robbins et al. 2013).

## 24.4.5 Social Behavior While on Land

The supplemental feeding of polar bears that occurs along Alaska's North Slope (see Chap. 21 for further detail) is an interesting example of how a seemingly benign human activity has altered the behavior of both bears and humans. Briefly, there are three communities along the North Slope (SB region) that hunt bowhead whales in the fall. The unused whale remains are aggregated into bone piles that then attract large numbers of bears (e.g., up to  $\approx 80$  individuals around a single location; Atwood et al. 2016b), mostly individuals that were summering onshore, but occasionally bears will make a long-distance swim from pack ice to a bone pile location (US Geological Survey, unpublished data). Only one bone pile (adjacent to the community of Kaktovik) is both consistently used and accessible enough to allow polar bear viewing, and a fledgling commercial bear-viewing industry has developed as a result. During peak viewing (which typically occurs in October), it is not uncommon for 10–20 tourists and local residents/day to use vehicles and boats to view bears feeding at the bone pile and resting at nearby barrier islands, respectively.

The demographic characteristics of polar bears visiting bone piles reflects that of the SB subpopulation, but there is some indication of demographic groups partitioning the use of bone piles relative to the presence of people, conspecifics, and allospecifics. For example, Miller et al. (2015) observed temporal partitioning of the Kaktovik bone pile, with lone adult polar bears and grizzly bears mostly feeding at night, while polar bear family groups (adult females with dependent young) and subadults fed mostly during dawn and dusk, when more people were usually present. Females with dependent young may not be more tolerant of the presence of people; rather they may be more wary of the presence of adult males given the potential for infanticide (Rode et al. 2006; Derocher and Wiig 1999). Conversely, adult males may be more wary of people given that they likely experience the greatest hunting pressure, as evidenced by the disproportional harvest of adult males (Derocher et al., 1997; Rode et al. 2006; Molnar et al., 2008). The observation that adult male bears resting on land near Churchill were more vigilant in the presence of tourists corroborates the idea of their elevated wariness of people (Dyck and Baydack 2004). Importantly though, it is unknown if competitive interactions or wariness of people interferes with feeding behavior at bone piles.

#### 24.4.6 Potential Impacts on Mating Success

Polar bears occur at low densities and range over vast areas, so they must rely on key behavioral traits to maximize the encounter of potential mates. As mentioned previously, movement data suggest that during the breeding season males minimize the likelihood of encountering each other, and maximize the likelihood of encountering females, by increasing the tortuosity of movement paths (Laidre et al. 2013). Additionally, ursids often rely on the deposition of scent marks on vertical substrates to communicate with conspecifics, but vertical features on sea ice are transient and make for poor substrates for chemical communication. Instead, there is evidence that polar bears may rely on pedal scent marking (via tracks left in snow) as a way to chemically communicate information (such as reproductive status) that may further facilitate encountering mates (Owen et al. 2015). However, the unpredictability of the Arctic sea ice, which has become more dynamic in spring as ice has thinned (Asplin et al. 2014), may impede the efficacy of these mate-searching behaviors by obstructing movement paths or disrupting scent trails. If conditions contributing to the impairment of mate-searching behaviors persist, it could increase the potential for Allee effects (i.e., a feature of small populations whereby low density limits individual fitness and population growth) in some subpopulations-especially those facing greater harvest pressure (in most subpopulations, males are harvested disproportionate to their abundance; see Chap. 25) (Molnar et al. 2008).

#### 24.5 Conclusions

Increasingly, human behavior is causing changes to the Arctic marine ecosystem. These changes are occurring indirectly through the influence of greenhouse gas emissions on physical processes that drive long-term change in ecosystem processes and directly via in situ activities that can immediately alter the behavior and fitness of wildlife. Some wildlife species will be able to adapt to these changes, while others may not possess the plasticity necessary to persist (Van Hemert et al. 2015). Polar bears have evolved preferences for sea ice habitat and for preving on marine mammals, which have shaped their behavioral traits. But the rapid changes taking place in the Arctic are making it more difficult for polar bears and other ice-adapted species to reliably use their traditional habitats and maintain fitness (e.g., Stirling and Derocher 2012; Derocher et al. 2013). Behavioral plasticity is the initial response to dramatic environmental perturbations, followed by transmission of innovative behaviors within and across generations, eventually leading to evolution of the behavioral response over time (Tuomainen and Candolin 2011). However, behavioral plasticity may be an effective response by polar bears only if the rate of environmental change does not outpace transmission of behavioral innovations. In short, it remains to be seen whether polar bears (1) possess the plasticity to cope with these changes and (2) will have sufficient time to innovate and adapt.

In some subpopulations, the lengthening open-water season already has been linked to declines in fitness and survival (Stirling et al. 1999; Regehr et al. 2010; Rode et al. 2010; Obbard et al. 2016). One of the purported mechanisms for these declines is prolonged food deprivation brought about by a lack of access to prey when sea ice is unavailable (Stirling and Derocher 2012). Polar bears have long possessed a feast-and-famine lifestyle, relying on fat reserves accumulated in the spring to ameliorate drastic declines in body condition during times when seals are less

available for capture. However, the plasticity of this lifestyle has limits. As mentioned earlier in this chapter, energy budget models indicate that an open-water period lasting >150 days could pose a substantial risk of reproductive failure and starvation. When ice is completely absent, bears will have no choice but to come ashore. The timing and pattern of sea ice melt and the presence of terrestrial-based food resources (e.g., Gormezano and Rockwell 2015; Rode et al. 2015) will largely determine when and where bears come ashore during the open-water period—some of these areas will be in close proximity to centers of human activities where food attractants are present. The eventual influx of a rising number of nutritionally stressed polar bears around coastal communities will likely result in increases in deaths from starvation, interspecific killing (e.g., Derocher and Wiig 1999), and human-bear conflict, all of which will challenge the limited capacities of managers.

Long-term projections of population status suggest that approximately twothirds of the world's polar bears could be lost by the middle of this century, unless the global mean temperature is held to  $\leq 2$  °C above preindustrial levels (Amstrup et al. 2008; Amstrup et al. 2010). It is important to note that there will be temporal variation in the responses of subpopulations to sea ice loss. Some subpopulations already have experienced the effects of sea ice loss (e.g., Regehr et al. 2007, 2010; Bromaghin et al. 2015), while others have remained stable during an initial period of sea ice loss (e.g., Rode et al. 2014). However, ultimately the projections of sea ice loss are so dramatic that it is unclear how bears will be able to persist long-term in most parts of their current range. Until greenhouse gas emissions are stabilized and further sea ice loss is stopped, management of in situ stressors may serve to slow the transition of populations to progressively worsened outcomes (Atwood et al. 2016a), thereby buying much needed time for polar bears to adapt to a new stable state and hopefully improve the prospects for their long-term persistence. Developing a more thorough understanding of polar bear behavior and their capacity for flexibility in response to anthropogenic disturbances and subsequent mitigations may lead to successful near-term management interventions.

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