

# The ecological and behavioral significance of short-term food caching in polar bears (*Ursus maritimus*)

Ian Stirling, Kristin L. Laidre, Andrew E. Derocher, and Rinie Van Meurs

**Abstract:** The paucity of observations of wild polar bears (*Ursus maritimus*) caching of food (including hoarding, i.e., burying and remaining with a kill for up to a few days) has led to the conclusion that such behavior does not occur or is negligible in this species. We document 19 observations of short-term hoarding by polar bears between 1973 and 2018 in Svalbard, Greenland, and Canada. Short-term hoarding appears to be influenced by size of the kill and its remaining energetic value after the first meal has been consumed. Fat and meat from smaller seals, such as pup or yearling ringed seals (*Pusa hispida*), are largely devoured immediately, leaving little to hoard. Carcasses of adult ringed seals, harp seals (*Pagophilus groenlandicus*), and bearded seals (*Erignathus barbatus*) may be covered with snow to reduce the chance of kleptoparasitism by another bear or other scavengers visually detecting a dark spot on the ice, while the hoarding bear lies nearby. Hoarding of other species, such as beluga (*Delphinapterus leucas*) (calves or parts) or other polar bears, appears opportunistic. We review differences in caching, including short-term hoarding behavior between polar bears and brown bears (*U. arctos*), and hypothesize about factors that may have influenced their evolution.

**Key words:** polar bear, caching, hoarding, predation, feeding, scavenging.

**Résumé :** Le manque d'observations sur des ours polaires (*Ursus maritimus*) qui conservent les restes de nourriture qu'ils ont capturée (dont le stockage, c.-à-d. enfouir et garder la dépouille d'une proie pendant une période allant jusqu'à quelques jours) a mené à la conclusion qu'un tel comportement ne survient pas ou qu'il est négligeable chez cette espèce. Les auteurs ont documenté 19 observations de stockage à court terme par des ours polaires entre 1973 et 2018 dans le Svalbard, au Groenland et au Canada. Le stockage à court terme semble influencé par la taille de la dépouille de la proie et sa valeur énergétique résiduelle lorsque le premier repas a été consommé. La graisse et la viande de plus petits phoques, comme le phoque annelé nouveau-né ou âgé d'un an (*Pusa hispida*) sont surtout dévorées immédiatement, laissant peu à stocker. Les carcasses de phoques annelés, de phoques du Groenland (*Pagophilus groenlandicus*) et de phoques barbus (*Erignathus barbatus*) adultes peuvent être recouvertes de neige, afin de réduire les risques de cleptoparasitisme par un autre ours ou par d'autres charognards qui détectent visuellement une tache noire sur la glace alors que l'ours qui a stocké ses réserves repose à proximité. Le stockage de restes d'autres

Received 19 June 2019. Accepted 10 October 2019.

**I. Stirling.** Wildlife Research Division, Department of Environment, Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada; Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

**K.L. Laidre.** Polar Science Center, Applied Physics Laboratory, University of Washington, Seattle, WA 98105, USA.

**A.E. Derocher.** Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

**R. Van Meurs.** Jastrzebia 201, 34-143 Lanckorona, Poland.

**Corresponding author:** Ian Stirling (e-mail: [Ian.Stirling@ualberta.ca](mailto:Ian.Stirling@ualberta.ca)).

This article is open access. This work is licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0). [http://creativecommons.org/licenses/by/4.0/deed.en\\_GB](http://creativecommons.org/licenses/by/4.0/deed.en_GB).

espèces comme le béluga (*Delphinapterus leucas*) (veau ou parties d'animal) ou d'autres ours polaires semble opportuniste. Les auteurs font la synthèse des différences de comportements de conservation de reste de nourriture capturée, dont le stockage à court terme, entre les ours polaires et les ours bruns (*U. arctos*) et formulent une hypothèse quant aux facteurs qui ont pu influencer leur évolution. [Traduit par la Rédaction]

*Mots-clés* : ours polaire, conservation de la nourriture capturée, stockage, prédation, alimentation, récupération.

## Introduction

Caching of food by terrestrial mammals, birds, and some insects for later use has been widely documented (see reviews by MacDonald 1976; Elgmork 1982; Smith and Reichman 1984; Vander Wall 1990; Sutton et al. 2016). Smith and Reichman (1984) concluded that caching occurs in species that bring food to their offspring and that caching is not undertaken by species in marine habitats. Although this generalization holds true for most marine species, observations of Weddell seals (*Leptonychotes weddellii*) and leopard seals (*Hydrurga leptonyx*) in Antarctica have confirmed that marine predators may cache prey but only for the short-term benefit of adults (Kim et al. 2005; Ponganis and Stockard 2007; Krause and Rogers 2019). Relevant to the behavior we describe below, Vander Wall's (1990) definition of caching includes short-term hoarding (i.e., burying and remaining with a kill for up to a few days), in which the locations of food items are hidden from sight from conspecifics or other species to facilitate consumption over a period of one to several days. Thus, we use the term "caching" to describe the short-term hoarding of prey (Vander Wall 1990) obtained by direct predation or scavenging by polar bears for their own consumption. A defining characteristic of the caching we document here was the continued presence of the bear.

Overall, there are few observations of caching in most species of bears (Ursidae), with the exception of brown bears (*Ursus arctos* Linnaeus, 1758), in which caching behavior, although little studied, has been reported frequently throughout Europe and North America (e.g., Murie 1981; Elgmork 1982; Barker and Derocher 2009; Cristescu et al. 2014). Caching by brown bears in Europe was apparently reported as early as 1599 (Storm 1881, cited by Elgmork 1982). Although caching by black bears (*U. americanus* Pallas, 1780) has also been reported (MacDonald 1965; Elgmork 1982), it appears to be uncommon. To our knowledge, caching behavior by polar bears (*U. maritimus* Phipps, 1774) has only been reported three times in the literature (Stirling 1974; Van Meurs 2005, p. 46; Aars et al. 2015, Fig. 1) and once as a personal communication citation by Elgmork (1982), but without any details. There have also been observations of surplus killing of seals by polar bears that simply abandon the carcasses without attempting to cache (Stirling and Derocher 1990; Smith and Stirling 2019). Polar bears are the most carnivorous of the ursids and rely predominantly on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) as their primary prey with additional, geographically variable, dietary contributions from harp seals (*Pagophilus groenlandicus*), walrus (*Odobenus rosmarus*), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) (Stirling and Archibald 1977; Smith and Sjare 1990; Thiemann et al. 2008).

We describe 19 observations of caching by polar bears, including the carcasses of three species of seals, parts of a beluga whale, a whole beluga calf, and partial carcasses of other polar bears. We discuss the possible biological significance of such behavior and consider factors that may influence the recognition and documentation of polar bear caching behavior in the field.

**Fig. 1.** (a) Adult male lying beside partially buried harp seal in northeastern Svalbard © J. Varley; (b) adult female polar bear with two cubs-of-the-year with adult ringed seal completely buried in northeastern Greenland © K.L. Laidre; (c) adult male standing over subadult bearded seal carcass while covering it with snow in the Barents Sea in northern Svalbard © R. Van Meurs; and (d) immobilized adult male lying beside beluga whale calf covered with grass except for fluke on the Manitoba coast of Hudson Bay © N.J. Lunn.



## Methods

Over the past 30 years, we used three methods to document polar bear behaviors on the sea ice: (1) from helicopters used to locate and capture large numbers of bears on the sea ice in spring and early summer for population studies in the Canadian Arctic, Greenland, and Svalbard (e.g., [Stirling and Archibald 1977](#); [Stirling et al. 1984](#); [Derocher et al. 2002](#); [Stirling 2002](#); [Pilfold et al. 2012](#); [Laidre et al. 2018a](#)); (2) searching with binoculars and telescopes from the decks of ecotourism ships in the pack ice in Svalbard (e.g., [Van Meurs 2005](#); [Smith and Stirling 2019](#)); and (3) long-term direct behavioral observations of undisturbed polar bears hunting on annual sea ice in the Canadian High Arctic (e.g., [Stirling 1974](#); [Stirling and Latour 1978](#)). In addition, opportunistic observations were documented on land near the coast from overland vehicles, helicopters, and foot travel during the open water period when the bears have few opportunities to hunt and most are fasting. Our observations of polar bears caching kills, or parts of scavenged animals, were documented descriptively, opportunistically, and in variable detail, depending on the circumstances. We were able to increase our sample size by accessing a small number of additional reliable observations and photographs as personal communications from scientific colleagues and photographers.

## Results

We documented 19 observations of caching behavior by wild polar bears.

*Observations of caching seals by polar bears:*

1. On 19 April 1987, 48 km southwest of Cape Bathurst in the southern Beaufort Sea, Canada (70.45°N, 127.08°W), while conducting a helicopter-based capture program, IS and AED immobilized a large thin adult male polar bear (21 years old) that had been feeding on a 200 cm adult bearded seal. Most of the skin and blubber had been removed from the back of the seal but none from the belly or sides. The bear had covered the carcass with snow scraped from the ice surface beside the carcass and was lying beside it. The bear was then captured as part of a long-term population study so there were no further observations of its behavior.
2. On 29 March 2016, while conducting a helicopter-based capture program near the coast in southeastern Greenland (approximately 64°N), KLL observed an adult male polar bear on land-fast ice actively caching an adult ringed seal. The carcass still had substantial meat and blubber on it (the skin and blubber had been removed from the back of the seal) and was mostly, but not completely, covered with snow. The bear was not captured but was re-sighted nearby several hours later.
3. On 7 July 2016, J. Varley (personal communication) sighted a large adult male polar bear asleep on a small ice floe beside a partially eaten and half-buried carcass of a harp seal in the pack ice (Fig. 1a) near Sjuøyane in northeastern Svalbard (approximately 81°N, 21°E). When the ship was about 150 m from the bear, it woke, dragged the carcass out from under its snow covering, left the floe he was on, swam with it to an adjacent floe, and dragged it out of the water. Between about 1930 and 2230 the bear moved the carcass several times, each time after which he slept briefly, washed his paws, fed, and re-buried the carcass.
4. On 9 April 2018, during a helicopter-based capture program, KLL observed an adult female with two cubs-of-the-year lying beside an adult ringed seal completely covered with snow (Fig. 1b) on the pack ice of East Greenland (approximately 75°N) around 0900. Six hours later, the bears were still at the site and the carcass was still covered with snow. When approached by the helicopter, the female ran to the cached carcass, pulled it out from under the snow and ran away with it in her mouth. The bears were captured so there were no additional observations.
5. From 2000 to 2018, while working on ecotourism ships, RVM documented eight instances of caching behavior. Six of the bears were large males, one was an unsexed subadult, and one was an adult female. Of the eight seals cached, one was a partially eaten adult ringed seal, one was a partially eaten and partially buried harp seal in open pack ice in the Barents Sea north of Svalbard (82°N and 22.50°E) (Fig. 1c), and six were bearded seals.
6. Between 1973 and 1990, during 155 bear days of continuous observations of undisturbed polar bears at Radstock Bay on the southwest coast of Devon Island, Nunavut (near 44.67°N; 91.25°W), 63 ringed seals were observed being killed and eaten (Stirling and Øritsland 1995). In only one case did a bear briefly attempt to scratch a small amount of snow, from the largely snow-free ice surface, over a largely eaten carcass (Stirling 1974).
7. Between 2000 and 2018, Dr. T.G. Smith spent parts of 14 late spring–summer seasons as a guide on ecotourism ships in Svalbard. During that period, he observed 400 bears, and 27 kills of a mixture of ringed, bearded, and harp seals, of which only one ringed seal was cached (personal communication). On 30 June 2008, along the southwest coast of Storfjorden, Svalbard (77°N; 17.3°E), a subadult polar bear was observed eating a ringed seal in jumbled pack ice. When the current pushed the ship toward the bear, it began to bury the carcass, and then remained with it until the ship left.



8. On 6 April 1989, Dr. Ø. Wiig (personal communication) caught an adult female polar bear that had recently buried an adult ringed seal that it had apparently caught within the previous 24 h on fast ice in Burgerbukta, Hornsund, Svalbard (77.03°N, 15.95°E). The fat on the back had been eaten but remained on the rest of the carcass.

*Observations of caching beluga by polar bears:*

1. On 19 September 2013, on the western coast of Hudson Bay (58.72°N; 93.17°W), Dr. N.J. Lunn (personal communication) caught an 18-year-old male polar bear in healthy condition lying beside an entire beluga calf completely covered with grass, except for the fluke, about 0.5 km from the coast (Fig. 1d). The carcass had been dragged inland from the beach but there was no blood in the area. Thus, it appeared the calf died elsewhere and had been washed to shore where it was found by the adult male. After the bear was darted for immobilization, it returned to the carcass, and lay down beside it, where he was when first sighted. The beluga carcass was then dragged back to the beach to reduce the risk of attracting other bears that might injure the drugged male while it was recovering. Two days later, the same male bear had dragged the carcass inland from the coast, back to the original site, re-covered it with grass, and was lying beside it again. Lunn later saw a second bear scavenging on a second beluga calf further down the coast but observed no caching behavior, although several other bears were in the area.
2. On 22 July 2006, RVM observed an adult female polar bear dragging a piece of beluga skin and fat, roughly 2 m long and 0.5 m wide in the pack ice approximately 10 km southeast of Sjuøyane in northeastern Svalbard (80.35°N; 22°E), north of Nordaustlandet, Svalbard. While the ship was present, the bear alternately buried the beluga skin, followed by digging it up, feeding and re-burying.

*Observations of caching of polar bear carcasses by polar bears:*

1. On 20 August 1997, RVM observed an adult male polar bear sleeping beside a partially covered, partially eaten, carcass of an adult female bear 200–300 m inland on a beach on Koldewey Island in Franz Josef Land, Russia (80.08°N, 59.1°E; Van Meurs 2005, p. 46). There was no evidence of a struggle, suggesting the bear had died before being scavenged by the adult male.
2. On 4 November 2016, AED observed an adult male polar bear standing over the unfrozen largely eaten remains of a yearling polar bear, partially covered with seaweed from the beach, on the western coast of Hudson Bay (58.78°N; 93.75°W). Its death was not witnessed but a large adult male was seen chasing a female with a yearling in the same area the previous day, although it was unknown if the same individual cached the remains. No subsequent observations were made.

## Discussion and conclusions

Using the methods described above, we have observed several thousand polar bears on Arctic pack and fast ice and similar numbers on land near the coast during the open water season, of which a very small number were observed with fresh seal kills or scavenging on other species.

The 19 instances of caching by polar bears that we report here are small when considered in relation to the large cumulative numbers of polar bears observed in a wide variety of locations, from different observation platforms, and over several decades. For example, of 27 seal kills observed on sea ice by Smith (this study), only one had been cached; of 650 seal kills documented on sea ice in the Beaufort Sea between 1985 and 2011 (Pilfold et al. 2012), only one observation of caching was documented (this study); and, of 63 seal kills observed

during long-term observations of undisturbed bears hunting on sea ice in spring and summer, caching was attempted only once ([Stirling and Øritsland 1995](#)).

#### **Influence of search method**

The greatest number of sightings of polar bears on sea ice are made from helicopters during large-scale tagging for population studies in spring (March–May), primarily on fast ice or compacted ice floes near the coast. In this circumstance, bears are usually first tracked and observed from the air at a distance in the air before being approached and then immobilized after a short pursuit. Unless there was visible evidence of a successful kill, such as blood in the snow, some of the locations where bears were first sighted were not re-visited. Even so, although we (IS, KL, and AED) conservatively estimate we have sighted >4000 polar bears during tagging as part of large-scale population studies on the sea ice, we documented only three instances of caching seals during those activities.

Of the 16 observations of caching behavior of seals by polar bears on the sea ice, it is notable that most (11) were sighted from ecotourism ships. When searching for bears, these ships move slowly while searching for distant animals on the ice that might be approached more closely to facilitate photography and observing their behavior. Thus, although the probability of observing caching behavior from a ship may be higher than from a helicopter, the frequency of occurrence is still low. From 2000 to 2018, three of us (RVM, IS, and T.G. Smith (personal communication)), spent significant portions of a total of 44 (often overlapping) spring–summer seasons as ecotourism guides searching for bears from different ships in Svalbard and observing the behavior of the bears sighted. Although, collectively on those trips, several hundred bears were sighted on the ice, we documented only 11 cached seals (including personal communication observations from colleagues included here).

It was not possible to make quantitative comparisons of the efficacy of making observations using different methods because of small sample sizes, the difficulty of quantifying the search effort, and because the data were collected opportunistically while applying the three different methods of search on the sea ice. Similarly, the small number of observations of caching by polar bears along the coast during the open water season when most bears were not actively hunting were sufficiently different to not warrant direct comparisons with those observed on the sea ice.

#### **Influence of size of animals cached**

Bears hunting on fast ice or larger areas of annual sea ice cover close to shore (prime habitat for ringed seals in winter and spring) are most likely to capture ringed seal pups and subadults ([Stirling and Archibald 1977](#); [Smith 1980](#); [Pilfold et al. 2012](#)), which are smaller than adult ringed, harp, or bearded seals. Importantly, because of their small size, kills of younger and smaller ringed seals are usually mostly consumed within an hour (unpublished observations from behavior study cited above ([Stirling and Øritsland 1995](#))) either by the successful hunter or by a larger bear that takes a fresh kill away from a smaller one. Consequently, in such cases there may not be enough remaining of the carcass to cache. Four of the five ringed seals we documented being cached on fast ice were adults, whereas the age class of the fifth was not recorded. In the pack ice, all the seals we reported cached were larger than pup or subadult ringed seals, whether they were adult ringed and harp seals or bearded seals of all ages. Although there were two adult harp seals in our sample, successful predation of that species in the pack ice is less common in Svalbard ([Derocher et al. 2002](#); [Smith and Stirling 2019](#)) so that bearded seals, which prefer open pack ice to fast ice ([Hamilton et al. 2017](#); [Breed et al. 2018](#); [Lone et al. 2018](#)) appear to be taken most frequently in that habitat and accounted for the largest fraction of both feeding and caching that we observed on the sea ice in late spring and early summer.

The observations of polar bears caching a beluga calf on land and a piece of beluga skin and fat on the pack ice, appear to have been opportunistic responses to finding animals that were already dead, or parts thereof. Similarly, the caching of the dead adult female polar bear by an adult male on land in Franz Josef Land appears to have been driven by finding a food source larger than could be consumed in one feeding. From the information available on the yearling polar bear cached on land on the Manitoba coast of Hudson Bay, it appeared to have been directly predated for food and already mostly eaten by the time it was observed. However, the observations on the behavior of that adult male bear were too brief, both before and after the yearling was killed, to be able to speculate more on the significance of the observation relative to caching behavior.

The unusual capture of white-beaked dolphins (*Lagenorhynchus albirostris*) while in a sassa (ice entrapment) by an adult male polar bear was observed in Svalbard, Norway (Aars et al. 2015). It is likely that the larger size of this carcass contributed to it having been cached and largely covered by snow. At least two of the observations of caching involved adult males in poor condition. Although our observations are inadequate to determine whether poor body condition increased the likelihood of caching, it is possible that such bears may be more likely to cache prey.

Regardless of the influence of other factors, the availability of snow with which to cover a carcass may also be a factor. Between 1975 and 1990, 63 seals were observed being killed and eaten by undisturbed wild polar bears in spring and early summer at Radstock Bay (Stirling and Øritsland 1995), plus an untallied number of bears attempting to scavenge later on the remains. Only one unsuccessful attempt to cache was observed, which was ineffective because of the small amount of snow on the bare summer sea ice. This suggests that the amount of snow available to cache the remains of a carcass with may be another factor influencing whether or not caching is attempted.

#### Possible evolutionary reasons for caching by polar and brown bears

Caching of food by terrestrial mammals for later use has been documented for a diversity of taxa, often for several days or more, to feed young (see reviews by MacDonald 1976; Smith and Reichman 1984). Polar bears are recently evolved from brown bears, which are well known to regularly cache kills or scavenged carcasses (e.g., Elgmork 1982). Thus, we propose that some of the differences in the caching or hoarding behavior by polar bears, compared with brown bears, may simply be that the lack of beneficial results over time has not been reinforced sufficiently for that behavior to be retained. Consequently, because caching or hoarding of prey taken by polar bears has rarely been reported in the scientific literature, it has largely been assumed to not occur (e.g., Amstrup 2003).

We suggest that the differences in caching behavior between the congeneric polar bear and brown bear may have been influenced by several factors (Table 1). In particular, the avian and mammalian scavenger community in terrestrial environments is diverse and may quickly consume a carcass when cached and left for some period by the successful predator (e.g., Hayes et al. 2000; Beasley et al. 2015). For example, it has been estimated that wolves (*Canis lupus*) may lose 2–20 kg of food per day to ravens (*Corvus corax*) (Vucetich et al. 2004). In another study, groups of ravens removed an estimated 37 kg of food per day from carcasses of wolf-killed prey (Promberger 1992).

In contrast, on the sea ice, many of the scavengers are small species in low numbers such as Arctic fox (*Vulpes lagopus*), gulls (Laridae), and ravens. Therefore, when hoarding, which appears to be the form of caching undertaken by most polar bears, the reduction or loss of part of a carcass to scavengers may be less of a threat to polar bears than it is for brown bears. In fact, the importance of remaining with a concealed or partially concealed carcass (i.e., hoarding) may simply be because of the greater threat of loss of food from a kill if it

**Table 1.** Factors that may affect caching and hoarding behaviour in the congeneric polar bear and brown bear.

Factors in caching	Polar bear	Brown bear	Comment
Food degradation	No	Yes	Variable for brown bears
Freezing of food	Yes	No/variable	—
Contribution of meat to diet	High	Low/variable	Spatial variation in brown bears (e.g., salmon, ungulate calves)
Prey source	Primarily active predation and secondarily scavenging	Primarily scavenging for larger prey and secondarily active predation	—
Visual hiding from conspecifics	Yes	Yes	—
Density of conspecifics	Low	High	—
Reduction of scent	Yes	Yes	—
Mass of prey relative to body mass	Low (less often high)	Variable	Ability to consume a high proportion of prey greater in polar bears
Diversity of avian scavengers	Low, Laridae and Corvidae	High, mainly Corvidae	—
Diversity of mammalian scavengers	Low, mainly Arctic fox	High, Canidae, Felidae, Ursidae, Mustelidae, Rodentia	—
Insect/microbe degradation	Low	High	—
Duration of cache	Hours to days	Days	—
Duration of feeding	Hours	Days	—
Availability of caching materials	Variable	High	—



was located, unguarded, by another polar bear. Incidental observations of captive bears indicate they can easily eat up to 10% of their body weight in 30 min (Best 1977), which illustrates the risk to a bear that might cache and leave a carcass unattended for an extended period.

Another notable difference between brown bears and polar bears is that brown bears hibernate through the coldest part of the year (e.g., Manchi and Swenson 2005), whereas polar bears (except for pregnant females in maternity dens) are active throughout the winter (e.g., Amstrup et al. 2000). During much of the time, cooler weather in polar regions might make carcasses last longer than in more temperate areas and, thus, make caching and hoarding more profitable. However, during the much colder conditions in which polar bears often hunt, the remains of prey are likely to freeze quickly so that feeding on frozen carcasses would increase handling time and decrease the energetic benefit because of the need to warm frozen tissue before consumption. Sometimes, during very cold weather, hard and totally frozen carcasses on the sea ice may be largely untouched by scavengers after the bear that made the kill was finished feeding and left the kill (I. Stirling, personal observation, 1986), simply because of the physical difficulties of tearing pieces free and then warming them sufficiently internally to obtain the energy. In general, polar bears occur at much lower densities (mean of 2.36 bears/1000 km<sup>2</sup>: Hamilton and Derocher 2019) than brown bears where densities range from 2 to 65 bears/1000 km<sup>2</sup> with most areas above 20 bears/1000 km<sup>2</sup> (Mowat et al. 2013). This difference suggests that intraspecific competition for carcasses may be much higher in brown bears, thus making the reduction of attractants more beneficial.

Even on the few occasions when caching does occur with polar bears, it appears to be for only for a few days at most though there are limited data available with which to quantify this aspect. Most of the animals cached are seals. From our limited observations, the small amount of caching documented appears to primarily involve carcasses too large for most or all of the fat and some meat to be devoured at a single feeding. Thus, carcasses such as those from adult ringed or harp seals, and especially bearded seals, may be partially or wholly covered with snow while the bear rests or sleeps nearby (e.g., Fig. 1a), feeds intermittently, and re-buries the carcass until there is little left to eat. Such caching probably does not exceed two or three days. It is likely that a carcass cached under snow reduces the probability that other scavengers detect it visually or by scent. Caching for later provisioning of young does not appear to occur although dependent cubs accompanying their mother at the time she caches a seal (Fig. 1b) may benefit from the cache. The small size of many of the nursing or newly weaned ringed seals caught in the fast ice may partially explain why fewer of the caching behaviors we observed were recorded there, compared to in the drifting pack ice where larger subadults and adults, mainly bearded seals, may be caught more often but are usually too large to be consumed at a single bout of feeding. It is also possible that some of the caching behavior may be specific to individuals or situations, such as densities of other bears, densities of scavengers, or even the length of time passed since it last caught a seal. However, the available data are inadequate to test these hypotheses.

During the most productive periods for hunting on annual fast ice, which is the prime habitat for ringed seals, a polar bear may, on average, only capture a seal about once in three days in April and May, and an average of once every five days in July, and longer at other seasons (Stirling and Øritsland 1995). In most cases, seals on the fast ice are small relative to the size of polar bears and the fat, skin, and a small amount of meat are devoured as quickly as possible after a kill has been made because of the possibility a larger bear may arrive and take the kill away or at least try to feed on it as well (Stirling 1974). Furthermore, because polar bears are capable of consuming 15%–20% of their body mass in a single meal (Best 1977), many seal kills may result in carcass remains that have limited energetic value, thus further reducing the potential benefits of caching and possibly having

to defend a cached carcass from another bear. To date, there are no data available on success rates for polar bears hunting in the drifting pack ice. Regardless, it appears that a large proportion of the bears hunting on either fast or pack ice have not fed recently (Cherry et al. 2009; Rode et al. 2018) and so would seize an opportunity to scavenge immediately if they were able to detect a carcass in the distance. The olfactory turbinal surface area of polar bears is exceptionally large for their body mass compared to other carnivores suggesting an acute sense of smell (Green et al. 2012). In comparison, using a trained Labrador retriever (*Canis lupus familiaris*), Smith and Stirling (1975) found that even ringed seal breathing holes or birth lairs beneath heavy snow drifts were readily detected by smell by the dog from measured distances of several hundred meters. Although there are no measured distances from which a polar bear is able to detect the remains of a seal by smell, such distances are likely to be greater than those documented from a Labrador retriever and the distances from which a cached carcass might be detectable to a bear would probably be further than for a breathing hole or birth lair beneath the snow.

Despite possessing a strong olfactory ability, a bear that might pass crosswind or upwind from a kill would probably need to see it before becoming aware of a scavenging opportunity. From observations of undisturbed polar bears hunting on the sea ice at Radstock Bay in the Canadian High Arctic, bears that see any dark object at distance usually investigate it (I. Stirling, personal observations, 1973–1976). Thus, it appears likely that one of the primary functions of covering a carcass with snow may be to make it more difficult to be seen by nearby bears.

It is also possible that total, but probably not partial, covering of a carcass makes it less detectable by avian scavengers, mainly gulls or ravens. Although scavenging birds usually feed on scraps away from where a bear is feeding on a carcass, other bears, seeing gulls or ravens on the sea ice at a distance, have likely learned that it is a sign of the presence of a carcass and may investigate.

Similarly, it seems likely that caching by polar bears of whole or partial carcasses of species like belugas or other bears is opportunistic and unlikely to result from specific searching. Although groups of polar bears feed together on beluga or other cetacean carcasses (Laidre et al. 2018b) such carcasses would be too large to cache by covering with snow. However, as reported above, if a sufficiently large piece can be removed from the original site, it may be enough to stimulate caching. However, such behavior is likely uncommon, even by the low frequency of caching in general by polar bears.

In summary, we conclude that caching behavior in polar bears is uncommon. That judgement is also supported by the paucity of references to caching behavior by polar bears in the scientific literature. Despite this, it appears from the diversity of the 19 observations presented here, caching behavior does occur in polar bears, albeit at a low frequency, across their range. Although small sample sizes and the opportunistic nature of the data collection preclude quantitative analyses, from a subjective examination of the data, it appears that the detectability of caching behavior may be influenced to some degree by the methods used to study polar bears, the type of habitat searched, the season, and the size of the prey or carcasses cached.

## Acknowledgements

We thank the Wildlife Research Division of Environment and Climate Change Canada, Polar Continental Shelf Project, Natural Sciences and Natural Science and Engineering Research Council (Ottawa), Department of Biological Sciences, University of Alberta, the Greenland Institute of Natural Resources, the Environmental Ministry of Denmark (DANCEA), and the Government of Greenland for long-term support of our research. G Adventures, Lindblad Expeditions, Oceanwide Expeditions, One Ocean Expeditions and

Quark Expeditions provided us with the opportunity to make many of the observations described above while we worked on their ships during ecotourism cruises. We are grateful to Dr. N.J. Lunn, Dr. T.G. Smith, Jenny Varley, and Dr. Ø. Wiig for permission to cite their unpublished observations and use their photographs. We thank David McGeachy, Wildlife Research Division, Environment and Climate Change Canada, for assistance with creation of the photo montage in Fig. 1.

## References

- Aars, J., Andersen, M., Brenière, M., and Blanc, S. 2015. White-beaked dolphins trapped in the ice and eaten by polar bears. *Polar Res.* **34**: 26612. doi: [10.3402/polar.v34.26612](https://doi.org/10.3402/polar.v34.26612).
- Amstrup, S.C. 2003. Polar bear, *Ursus maritimus*. In *Wild mammals of North America: biology, management, and conservation*. 2nd ed. Edited by G.A. Feldhamer, B.C. Thompson, and J.A. Chapman. Johns Hopkins University Press, Baltimore, Md., USA. pp. 587–610.
- Amstrup, S.C., Durner, G.M., Stirling, I., Lunn, N., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Can. J. Zool.* **78**: 948–966. doi: [10.1139/z00-016](https://doi.org/10.1139/z00-016).
- Barker, O.E., and Derocher, A.E. 2009. Brown bear (*Ursus arctos*) predation of broad whitefish (*Coregonus nasus*) in the Mackenzie Delta Region, Northwest Territories. *Arctic*, **62**: 312–316. doi: [10.14430/arctic151](https://doi.org/10.14430/arctic151).
- Beasley, J.C., Olson, Z.H., and DeVault, T.L. 2015. Ecological role of vertebrate scavengers. In *Carion ecology, evolution, and their applications*. Edited by M.E. Benbow, J.K. Tomberlin, and A.M. Tarone. CRC Press, Boca Raton, Fla., USA. pp. 107–127.
- Best, R.C. 1977. Ecological aspects of polar bear nutrition. In *Proceedings of the 1975 Predator Symposium*. Edited by R.L. Phillips and C. Jonkel. University of Montana Press, Missoula, Mont., USA. pp. 203–211.
- Breed, G.A., Cameron, M.F., Ver Hoef, J.M., Boveng, P.L., Whiting, A., and Frost, K.J. 2018. Seasonal sea ice dynamics drive movement and migration of juvenile bearded seals *Erignathus barbatus*. *Mar. Ecol. Progr. Ser.* **600**: 223–237. doi: [10.3354/meps12659](https://doi.org/10.3354/meps12659).
- Cherry, S.G., Derocher, A.E., Stirling, I., and Richardson, E.S. 2009. Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea. *Polar Biol.* **32**(3): 383–391. doi: [10.1007/s00300-008-0530-0](https://doi.org/10.1007/s00300-008-0530-0).
- Cristescu, B., Stenhouse, G.B., and Boyce, M.S. 2014. Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. *Anim. Behav.* **92**: 133–142. doi: [10.1016/j.anbehav.2014.03.020](https://doi.org/10.1016/j.anbehav.2014.03.020).
- Derocher, A.E., Wiig, Ø., and Andersen, M. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biol.* **25**: 448–452. doi: [10.1007/s00300-002-0364-0](https://doi.org/10.1007/s00300-002-0364-0).
- Elgmork, K. 1982. Caching behavior of brown bears (*Ursus arctos*). *J. Mammal.* **63**: 607–612. doi: [10.2307/1380265](https://doi.org/10.2307/1380265).
- Green, P.A., Van Valkenburgh, B., Pang, B., Bird, D., Rowe, T., and Curtis, A. 2012. Respiratory and olfactory turbinal size in canid and arctoid carnivores. *J. Anat.* **221**: 609–621. doi: [10.1111/j.1469-7580.2012.01570.x](https://doi.org/10.1111/j.1469-7580.2012.01570.x). PMID: 23035637.
- Hamilton, C.D., Kovacs, K.M., Ims, R.A., Aars, J., Strøm, H., and Lydersen, C. 2017. Spatial overlap among an Arctic predator, prey and scavenger in the marginal ice zone. *Mar. Ecol. Progr. Ser.* **573**: 45–59. doi: [10.3354/meps12184](https://doi.org/10.3354/meps12184).
- Hamilton, S.G., and Derocher, A.E. 2019. Assessment of global polar bear abundance and vulnerability. *Anim. Conserv.* **22**: 83–95. doi: [10.1111/acv.12439](https://doi.org/10.1111/acv.12439).
- Hayes, R.D., Baer, A.M., Wotschikowsky, U., and Harestad, A.S. 2000. Kill rate by wolves on moose in the Yukon. *Can. J. Zool.* **78**: 49–59. doi: [10.1139/cjz-78-1-49](https://doi.org/10.1139/cjz-78-1-49).
- Kim, S.L., Conlan, K., Malone, D.P., and Lewis, C.V. 2005. Possible food caching and defence in the Weddell seal: observations from McMurdo Sound, Antarctica. *Antarct. Sci.* **17**: 71–72. doi: [10.1017/S0954102005002452](https://doi.org/10.1017/S0954102005002452).
- Krause, D.J., and Rogers, T.L. 2019. Food caching by a marine apex predator, the leopard seal (*Hydrurga leptonyx*). *Can. J. Zool.* **97**: 573–578. doi: [10.1139/cjz-2018-0203](https://doi.org/10.1139/cjz-2018-0203).
- Laidre, K.L., Born, E.W., Atkinson, S.N., Wiig, Ø., Andersen, L.W., Lunn, N.J., et al. 2018a. Range contraction and increasing isolation of a polar bear subpopulation in an era of sea ice loss. *Ecol. Evol.* **8**: 2062–2075. doi: [10.1002/ece3.3809](https://doi.org/10.1002/ece3.3809).
- Laidre, K.L., Stirling, I., Estes, J.A., Kochnev, A., and Roberts, J. 2018b. Historical and potential future importance of large whales as food for polar bears. *Front. Ecol. Environ.* **16**: 515–524. doi: [10.1002/fee.1963](https://doi.org/10.1002/fee.1963).
- Lone, K., Merkel, B., Lydersen, C., Kovacs, K.M., and Aars, J. 2018. Sea ice resource selection models for polar bears in the Barents Sea subpopulation. *Ecography*, **41**: 567–578. doi: [10.1111/ecog.03020](https://doi.org/10.1111/ecog.03020).
- MacDonald, D.W. 1976. Food caching by red foxes and some other carnivores. *Z. Tierpsychol.* **42**: 170–185. doi: [10.1111/j.1439-0310.1976.tb00963.x](https://doi.org/10.1111/j.1439-0310.1976.tb00963.x). PMID: 1007654.
- MacDonald, W.H. 1965. Bears and people. *Land For. Wildl.* **8**: 16–32. Cited in: Cardoza, J.E. 1976. The history and status of the black bear in Massachusetts and adjacent New England states. Massachusetts Division of Fisheries and Wildlife Research Bulletin No. 18. 113 pp.
- Manchi, S., and Swenson, J.E. 2005. Denning behaviour of Scandinavian brown bears *Ursus arctos*. *Wildl. Biol.* **11**: 123–132. doi: [10.2981/0909-6396\(2005\)11\[123:DBOSBB\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[123:DBOSBB]2.0.CO;2).
- Mowat, G., Heard, D.C., and Schwarz, C.J. 2013. Predicting grizzly bear density in western North America. *PLoS ONE*, **8**(12): e82757. doi: [10.1371/journal.pone.0082757](https://doi.org/10.1371/journal.pone.0082757). PMID: 24367552.
- Murie, A. 1981. The grizzlies of Mount McKinley. U.S. Department of the Interior, National Park Service, Washington, D.C., USA. 251 pp.

- Pilfold, N.W., Derocher, A.E., Stirling, I., Richardson, E., and Andriashek, D. 2012. Age and sex composition of seals killed by polar bears in the eastern Beaufort Sea. *PLoS ONE*, 7: e41429. doi: [10.1371/journal.pone.0041429](https://doi.org/10.1371/journal.pone.0041429). PMID: 22829949.
- Ponganis, P.J., and Stockard, T.K. 2007. Short Note: the Antarctic toothfish: how common a prey for Weddell seals? *Antarct. Sci.* 19: 441–442. doi: [10.1017/S0954102007000715](https://doi.org/10.1017/S0954102007000715).
- Promberger, C. 1992. Wolfe und Scavenger. Diplomarbeit, Ludwig Maximilians Universität, München, Germany.
- Rode, K.D., Wilson, R.R., Douglas, D.C., Muhlenbruch, V., Atwood, T.C., Regehr, E.V., et al. 2018. Spring fasting behavior in a marine apex predator provides an index of ecosystem productivity. *Glob. Change Biol.* 24: 410–423. doi: [10.1111/gcb.13933](https://doi.org/10.1111/gcb.13933).
- Smith, C.C., and Reichman, O.J. 1984. The evolution of food caching by birds and mammals. *Annu. Rev. Ecol. Syst.* 15: 329–351. doi: [10.1146/annurev.es.15.110184.001553](https://doi.org/10.1146/annurev.es.15.110184.001553).
- Smith, T.G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. *Can. J. Zool.* 58: 2201–2209. doi: [10.1139/z80-302](https://doi.org/10.1139/z80-302).
- Smith, T.G., and Sjøre, B. 1990. Predation of belugas and narwhals by polar bears in nearshore areas of the Canadian High Arctic. *Arctic*, 43: 99–102. doi: [10.14430/arctic1597](https://doi.org/10.14430/arctic1597).
- Smith, T.G., and Stirling, I. 1975. The breeding habitat of the ringed seal (*Phoca hispida*): the birth lair and associated structures. *Can. J. Zool.* 53: 1297–1305. doi: [10.1139/z75-155](https://doi.org/10.1139/z75-155).
- Smith, T.G., and Stirling, I. 2019. Predation of harp seals, *Pagophilus groenlandicus*, by polar bears, *Ursus maritimus*, in Svalbard. *Arctic*, 72: 197–202. doi: [10.14430/arctic68186](https://doi.org/10.14430/arctic68186).
- Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). *Can. J. Zool.* 52: 1191–1198. doi: [10.1139/z74-157](https://doi.org/10.1139/z74-157).
- Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic*, 55(Suppl. 1): 59–76.
- Stirling, I., and Archibald, W.R. 1977. Aspects of predation of seals by polar bears. *J. Fish. Res. Board Can.* 34: 1126–1129. doi: [10.1139/f77-169](https://doi.org/10.1139/f77-169).
- Stirling, I., and Derocher, A.E. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. *Bears*, 8: 189–204. doi: [10.2307/3872919](https://doi.org/10.2307/3872919).
- Stirling, I., and Latour, P.B. 1978. Comparative hunting abilities of polar bear cubs of different ages. *Can. J. Zool.* 56: 1768–1772. doi: [10.1139/z78-242](https://doi.org/10.1139/z78-242).
- Stirling, I., and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* 52: 2594–2612. doi: [10.1139/f95-849](https://doi.org/10.1139/f95-849).
- Stirling, I., Calvert, W., and Andriashek, D. 1984. Polar bear ecology and environmental considerations in the Canadian High Arctic. In *Northern ecology and resource management*. Edited by R. Olson, F. Geddes, and R. Hastings. University of Alberta Press, Edmonton, Alta., Canada. pp. 201–222.
- Sutton, A.O., Strickland, D., and Norris, D.R. 2016. Food storage in a changing world: implications of climate change for food-caching species. *Clim. Change Responses*, 3: 12. doi: [10.1186/s40665-016-0025-0](https://doi.org/10.1186/s40665-016-0025-0).
- Thiemann, G.W., Iverson, S.J., and Stirling, I. 2008. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecol. Monogr.* 78: 591–613. doi: [10.1890/07-1050.1](https://doi.org/10.1890/07-1050.1).
- Van Meurs, R. 2005. Polar bears of Spitsbergen/Svalbard. *Oceanwide Expeditions*, Vlissingen, the Netherlands. 64 pp.
- Vander Wall, S.B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Ill., USA.
- Vucetich, J.A., Peterson, R.O., and Waite, T.A. 2004. Raven scavenging favours group foraging in wolves. *Anim. Behav.* 67: 1117–1126. doi: [10.1016/j.anbehav.2003.06.018](https://doi.org/10.1016/j.anbehav.2003.06.018).