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NOTE

**Predation on ringed seals in subnivean lairs in northwest Alaska during spring 1983 and 1984**

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The ringed seal (*Pusa hispida*) is a small pagophillic ("ice loving") arctic phocid. It is an abundant and circumpolar species that plays a central role in arctic marine ecosystems, with life history patterns that are strongly influenced by seasonal patterns of sea ice and snow cover (Burns, 1970; McLaren, 1958; Smith, 1987). During winter, ringed seals maintain breathing holes in landfast and dense pack ice habitats and excavate subnivean ("under the snow") lairs on the ice surface (Smith & Stirling, 1975). Pups are born in lairs in April or May and nurtured within the lair before weaning within 5-6 weeks (Hammill et al., 1991; Smith et al., 1991). Lairs provide protection from wind and cold (Smith et al., 1991) as well as concealment from predators (Hammill & Smith, 1991; Smith, 1976, 1980; Smith & Lydersen, 1991; Stirling & Archibald, 1977) until the snow melts and lairs collapse.

Polar bears (*Ursus maritimus*) and arctic foxes (*Vulpes lagopus*), hunt and kill ringed seals in their lairs on the sea ice in spring (Lydersen & Gjertz, 1986; Smith, 1976, 1980; Smith & Hammill, 1981; Smith & Stirling, 1975; Stirling & Archibald, 1977). Although seals constitute a year-round primary prey item for bears (Stirling, 2002), both bears and foxes rely on visual and olfactory cues to hunt pups in spring; they enter lairs to kill pups before they can escape into the water. When hunting

ringed seals in lairs, bears search along pressure ridges, deformed ice, or along refrozen cracks before pouncing on the overlying snow to collapse the roof of a lair (Stirling & McEwan, 1975). Deep snow can decrease bear predation attempts and success rates (Hammill & Smith, 1991), particularly as the thickness of lair roofs increase (Furgal et al., 1996). Arctic foxes are significant predators of pups in lairs in much of the geographic range of ringed seals (Smith, 1976; Smith et al., 1991). They gain entrance to lairs by digging small holes into the roof. Foxes also scavenge seal remains left by polar bears (Lydersen & Gjertz, 1986).

Here, we report data about predation of pups in lairs on landfast ice in two regions of northwest Alaska. These historical and previously unpublished findings, obtained in 1983 and 1984, predate the contemporary period of dramatic sea ice loss and climatic change in the eastern Chukchi Sea region (Huntington et al., 2020), providing a benchmark to which current and future conditions can be compared. Our objective is to describe the magnitude of bear and fox predation and kill rates for different types of subnivean structures in two regions of northwest Alaska. These results will be compared with similar studies conducted across the circumpolar Arctic and discussed in the context of recent environmental changes.

Specially trained Labrador retriever dogs were used to search for ringed seal structures on landfast sea ice in two regions of the eastern Chukchi Sea: southern Kotzebue Sound (~66°16'N, 162°32'W) and ~130 nautical miles farther north in Ledyard Bay (~68°53'N, 165°50'W) (Figure 1). Surveyed grids were searched in Kotzebue Sound during April 5-29, 1983 (two study grids) and in Ledyard Bay during April 6 to May 13, 1984 (five study grids), as described elsewhere (Frost & Burns, 1989; Hauser et al., 2021). Ringed seal structures were measured and classified as breathing holes, haul-out lairs, complex, or pup lairs. Complex and pup lairs were combined for the purposes of this analysis (Hauser et al., 2021), and are hereafter referred to as pup lairs. Modern geospatial tools were also used to locate each structure within a study grid and its proximity to other structures (see Hauser et al., 2021).

At each structure, any evidence of fox or bear presence was documented. Notations included whether there were indications that a structure had been visited (urine or feces, tracks), entered but no kill made (tunnels or demolished by external force), or a seal killed (remains of a seal or blood) at a structure. We summarized the proportion of structures that were visited, entered but without a kill, and where a kill occurred according to predator, type of structure, and study grid.

Predation rates for each predator and grid were calculated as the number of seal kills per km<sup>2</sup> surveyed.

Overall, there were substantial differences in the incidence of predator activity among study areas (Figure 1). Bears or foxes visited, entered, or killed seals at a total of 142 seal structures, or 29% of the 490 structures (Table 1). A total of 15 seals (at 3% of all structures) were killed.

There was sign of arctic fox presence or predation at a total of 120 seal structures (Table 1). Foxes visited or entered all kinds of structures but made kills primarily at pup lairs (Figure 2). Fox sign was evident at far more seal structures in Ledyard Bay ( $n = 112$ , 45% of structures) than in Kotzebue Sound ( $n = 8$ , 3% of structures). Foxes visited 58 (23%), entered 44 (18%), and killed seals at 10 (4%) structures in Ledyard Bay. All fox kills in Ledyard Bay were pups in lairs. In Kotzebue Sound, foxes visited three (1%) and entered 4 (2%) structures. One pup (0.4% of structures) was killed in grid 1983-2. Melt was well underway at the time grid 1983-2 was surveyed and it was difficult to see fox tracks as well as to conduct searches of ringed seal structures (see Hauser et al., 2021).

Polar bears visited, entered, or killed seals at a total of 22 structures (Table 1). There was no indication of the presence of polar bears in Kotzebue Sound. In Ledyard Bay, polar bears

visited 7 (3%), entered 11 (4%), and made kills at 4 (2%) structures. Three of the four pups killed were in pup lairs. The remains of the fourth pup were found ~30 m away from a cluster of lairs, including a pup lair that had been opened by a bear. Most signs of bear predation were in Ledyard Bay grid 1984-1 ( $n = 18$ , 82% of total structures visited or entered). Grid 1984-1 was located directly seaward of a polar bear den from which a sow and two cubs of the year emerged in mid-April. The sow was seen actively hunting within grid 1984-1. Bears visited 6%, entered 10% but did not kill, and made kills at 3% of the 93 seal structures in grid 1984-1. There were also three kills by foxes, resulting in a combined predation rate of 0.55 kills/km<sup>2</sup> in grid 1984-1. Polar bears also visited, entered, or killed seals at structures in grids 1984-3 ( $n = 2$ ) and 1984-4 ( $n = 2$ ).

There were signs of both foxes and bears at nine seal structures in Ledyard Bay: eight in grid 1984-1 and one in grid 1984-4. Of these nine structures, three were kills by bears that were also visited by foxes. One was a kill by a fox that was visited by a bear. One additional pup lair was entered by a fox and had bear tracks, but there was no evidence of a kill. Overall, bears and foxes killed a total of 15 seals and had a combined predation rate of 0.23 kills/km<sup>2</sup> (Table 2). The predation rate in Ledyard Bay (0.46 kills/km<sup>2</sup>) was much higher

than it was in Kotzebue Sound (0.03 kills/km<sup>2</sup>). In Ledyard Bay, the fox kill rate (0.33 kills/km<sup>2</sup>, range 0-0.74 kills/km<sup>2</sup>) was higher than the bear kill rate (0.13 kills/km<sup>2</sup>, range 0-0.27 kills/km<sup>2</sup>). However, foxes had fewer kills per visits (17%) than did bears (57%) overall in Ledyard Bay (Table 1), presumably because bears are more effective predators of pups in lairs.

The different predation rates by polar bears and arctic foxes in the study grids likely reflects annual variations as well as regional differences in abundance of both species. Polar bear predation on ringed seals only occurred in the Ledyard Bay region, where bears were common during the winter-spring of 1983-1984, as reflected in harvest records (Frost & Burns, 1989). Decades of telemetry data (e.g., Wilson et al., 2016), in addition to local and Indigenous Knowledge (A. Whiting, personal communication, August 16, 2021), confirm that polar bears rarely occur in Kotzebue Sound. Kotzebue Sound is a large shallow estuarine embayment with substantial freshwater input from four major rivers. Ledyard Bay, in comparison, is a wide coastal indentation facing northward and open to the broader Chukchi Sea with a flaw lead system that historically occurred several kilometers offshore. The ice edge, lead system, and offshore pack ice provide additional foraging opportunities for polar bears, which also prey on nonpup ringed seals found in this

habitat.

Arctic fox predation of ringed seals occurs on pups at lairs in spring (Smith, 1976, 1980; Smith & Lydersen, 1991; Stirling, 2002; Stirling & Archibald, 1977). In this study, foxes also visited breathing holes and haul-out lairs, however all but one kill occurred at pup lairs. Fox presence was quite variable among study grids, as indicated by tracks and other marks. Arctic fox abundance is thought to vary predominantly in relation to the abundance of lemmings (*Dicrostonyx* and *Lemmus* spp.), their primary terrestrial prey (Macpherson, 1969). However, seal pups subsidize the diet of foxes (Roth, 2002) to the extent that consumption of ringed seal carrion and predation on pups can moderate fox abundance even in years with low terrestrial prey availability (Roth, 2003). Lemming densities also play a broader ecological role in moderating fox predation on other species: in years of low lemming abundance, Steller's eiders (*Polysticta stelleri*) in northern Alaska may forego breeding due to increased fox predation pressure (Quakenbush et al., 2004). We do not have additional information on fox or lemming abundance in our study region. However, trappers in several nearby communities observed that foxes were not abundant during the winters of 1983-1984 when our study took place (Frost & Burns, 1989).



During spring, polar bear predation of ringed seals in the fast ice is focused on pups in lairs (Smith, 1976, 1980; Smith & Lydersen, 1991; Stirling, 2002; Stirling & Archibald, 1977). Bears have poor success capturing adult seals at subnivean structures and often leave unoccupied lairs undisturbed, suggesting that bears can distinguish pup lairs from other structures as well as whether a lair is occupied (Hammill & Smith, 1991; Smith, 1980; Stirling & Archibald, 1977). Furgal et al. (1996) found that longer and wider subnivean structures, characteristic of lairs with pups, were more likely to be entered by foxes and bears, and that haul-out lairs with strong *tiggak* odors of rutting male ringed seals (Smith & Stirling, 1975) were avoided. In our study, polar bears visited all types of structures, but primarily entered lairs where they killed pups. *Tiggak* odors were not documented at any of the structures visited by predators in our study.

Kill rates and predation pressure vary according to interannual and regional variability in habitat conditions as well as predator and prey abundance and distribution. A review of studies conducted across the geographic range of ringed seals reveals wide ranges in predation pressure (Table 3, also see Furgal et al., 1996; Hammill & Smith, 1991). The percent of kills made by polar bears in the Ledyard Bay study area (2% of

structures) was similar to that in Svalbard (1%), Admiralty Inlet (0%-3%), Barrow Strait (2%-8%), southeast Baffin Island (0%-7%), and Amundsen Gulf (0%-1%) regions of the Canadian Arctic. Some regions reported no bear predation at lairs, including our study area in Kotzebue Sound where bears are rare. Reported fox predation rates at lairs were also variable, ranging from none in the Barrow Strait region to 4%-8% in Ledyard Bay, Amundsen Gulf, and Svalbard (Table 3).

Annual variability in predation rates was also substantial. For example, in Admiralty Inlet, bears entered and killed seals in 1992 but not in 1991 or 1993 (Furgal et al., 1996). Foxes entered 0%, 7%, and 24% of structures during those three years but rarely made a kill. The overall kill rate over 1991-1993 (0.02 kills/km<sup>2</sup> surveyed) was lower than rates in our study areas and in 3 years of study in Barrow Strait (Hammill & Smith, 1989). In Barrow Strait, kill rates of pups in 1984 were low and similar to Kotzebue Sound (0.03 kills/km<sup>2</sup> surveyed) but higher (0.48 kills/km<sup>2</sup>) and similar to Ledyard Bay (0.46 kills/km<sup>2</sup> surveyed) in 1986, further illustrating how variable predation pressure can be among years for a given region. Hammill and Smith (1991) noted that only a single kill was found prior to the mean pupping date of April 21 during studies in Barrow Strait, and predation rates of pups, recalculated for plots

surveyed after the mean pupping date, were 0.11, 0.3, 0.74 pups/km<sup>2</sup> in 1984, 1985, and 1986, respectively. They estimated that polar bears removed 4%-20% of the ringed seals present, including 8%-44% of the pups born in those years. Sharp increases in polar bear predation rates in Barrow Strait occurred from 1984 to 1985 as mean snow depths declined from 23 cm to 10 cm. Higher densities of bears in 1986 were assumed to be due to closer proximity to open water (Ramsay & Stirling, 1986). Overall, both seal and predator abundance and densities are known to fluctuate relative to their variable ice and snow habitats (Frost et al., 2004; Harwood et al., 2000; Stirling, 2002). Estimates of predation rates can also vary by the number of replicate surveys conducted at a site during a given study (Hammill & Smith, 1991). Results based on a single survey may overestimate predation success due to greater detectability of carcasses by the search dogs, although each grid in our study was searched at least two or more times until no additional seal structures were found (Hauser et al., 2021).

Climate change has resulted in rapid shifts in phenology and unprecedented loss of the quality, quantity, and extent of ice and snow habitat available to ringed seals from the 1970s to the 1990s when most ringed seal lair studies were conducted. These changes have almost certainly affected predation rates.

Subnivean lairs provide ringed seal pups critical shelter from severe weather and predators. Reduction of sea ice extent, thickness, and duration of cover across the Arctic (Comiso et al., 2017; Stroeve & Notz, 2018; Stroeve et al., 2014) has been accompanied by projections of decreasing snow depth on sea ice (Hezel et al., 2012; Webster et al., 2021) that may affect construction of subnivean lairs. Lairs with thin "roofs" could melt prematurely or have less structural integrity, so pups may have reduced survival due to increased predation or weather exposure (Lukin & Potelov, 1978/1979). During unusual warm temperatures and rain events on southeast Baffin Island in April 1972, lairs collapsed prematurely and pups exposed in their subnivean lairs experienced elevated rates of bear and fox predation (Stirling & Smith, 2004). In Svalbard, pups born outside of lairs in areas with insufficient snow cover are additionally exposed to avian predators (Gjertz & Lydersen, 1986; Lydersen & Smith, 1989). During recent years (2018 and 2019), anomalously thin and less extensive landfast ice cover in Kotzebue Sound, coupled with widespread surface flooding of the ice, may have also impacted availability of subnivean lair habitat suitable for pup thermal and predator protection (Mahoney et al., 2021). Ultimately, lairs provide a physical barrier reducing access by predators, and deeper snow provides

thicker roofs and therefore greater protection of pups from predators (Furgal et al., 1996; Hammill & Smith, 1991).

Additional work is needed to understand how changing snow depths and ice cover will affect subnivean lairs that protect ringed seal pups from predators.

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was conducted on the landfast ice within the traditional and ongoing territories of Alaska's Iñupiaq people. We acknowledge their stewardship and appreciate the Iñupiaq hunters from the communities of Deering and Point Hope, Alaska who supported and contributed to this work.

The data that support the findings of this study are openly available: <https://search.dataone.org/view/10.24431/rw1k5b3>

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**TABLE 1** Frequency and percent of detected ringed seal structures with signs of polar bears or arctic foxes visiting, entering, or kills during seal structure surveys in Kotzebue Sound and Ledyard Bay, Alaska.

	Polar bear				Arctic fox			
	Visit <i>n</i> (%)	Enter <i>n</i> (%)	Kill <i>n</i> (%)	Total <i>n</i> (%)	Visit <i>n</i> (%)	Enter <i>n</i> (%)	Kill <i>n</i> (%)	Total <i>n</i> (%)
Kotzebue Sound (April 1983)								
Breathing hole ( <i>n</i> = 84)								
Haul-out lair ( <i>n</i> = 97)					1 (<1%)	4 (2%)		5 (2%)
Pup lair ( <i>n</i> = 59)					2 (1%)		1 (<1%)	3 (1%)
Total ( <i>n</i> = 242) <sup>a</sup>					3 (1%)	4 (2%)	1 (<1%)	8 (3%)
Ledyard Bay (April–May 1984)								
Breathing hole ( <i>n</i> = 62)	3 (1%)	1 (<1%)		4 (2%)	9 (4%)	3 (1%)		12 (5%)
Haul-out lair ( <i>n</i> = 102)	1 (<1%)	7 (3%)	1 (<1)	9 (4%)	25 (10%)	19 (8%)	1 (<1%)	45 (18%)
Pup lair ( <i>n</i> = 82)	2 (1%)	3 (1%)	3 (1%)	8 (3%)	23 (9%)	22 (9%)	9 (4%)	54 (22%)
Unclassified lair ( <i>n</i> = 2)	1 (<1%)			1 (<1%)	1 (<1%)			1 (<1%)
Total ( <i>n</i> = 248)	7 (3%)	11 (4%)	4 (2%)	22 (9%)	58 (23%)	44 (18%)	10 (4%)	112 (45%)
Overall total ( <i>n</i> = 490)	7 (1%)	11 (2%)	4 (1%)	22 (4%)	61 (12%)	48 (10%)	11 (2%)	120 (24%)

<sup>a</sup> Includes two unclassified lairs, neither of which had signs of predation.



**TABLE 2** Rates of ringed seal kills by arctic foxes and polar bears in study grids within Kotzebue Sound (KS) and Ledyard Bay (LB) regions.

<b>Grid</b>	<b>Area (km<sup>2</sup>)</b>	<b>Fox kills</b>	<b>Bear kills</b>	<b>Fox predation rate (kills/km<sup>2</sup>)</b>	<b>Bear predation rate (kills/km<sup>2</sup>)</b>	<b>Total kills</b>	<b>Overall predation rate (kills/km<sup>2</sup>)</b>
1983-1	27.37	0	0	0	0.00	0	0.0
1983-2	5.87	1	0	0.17	0.00	1	0.17
KS Total	33.24	1	0	0.03	0.00	1	0.03
1984-1	10.92	3	3	0.27	0.27	6	0.55
1984-2	5.32	0	0	0	0.00	0	0.00
1984-3	5.43	4	0	0.74	0.00	4	0.74
1984-4	5.56	2	1	0.36	0.18	3	0.54
1984-5	3.4	1	0	0.29	0.00	1	0.29
LB total	30.63	10	4	0.33	0.13	14	0.46
Total	63.87	11	4	0.17	0.06	15	0.23

**TABLE 3** Comparisons of predator predation attempts (entered) and kills at ringed seals structures from surveys across their geographic range, based on studies conducted on the landfast ice during the pupping season using trained dogs.

Region	Year(s)	Number of structures ( <i>n</i> )	Polar bears		Arctic fox		Pup predation rate (pup kills/km <sup>2</sup> surveyed)	Source
			Attempts (%)	Kills (%)	Attempts (%)	Kills (%)		
Kotzebue Sound, NW Alaska	April–May 1983	242	0	0	2	<1	0.03	This study
Ledyard Bay, NW Alaska	April–May 1984	248	4	2	18	4	0.46	This study
Beaufort Sea, N Alaska	March–April 1982	73	0	0	19	<1	—	Kelly et al. (1986)
	March–April 1983	37	0	0	<1	0	0	
Amundsen Gulf, W Canada	1972	85	0	0	—	—	—	Smith (1980) <sup>a</sup>
	1973	78	5	1	—	—	—	
	1974	122	0	0	—	—	—	
	1975	25	4	0	—	—	—	Smith (1976) <sup>c</sup>
	March–June 1972–1975	370	—	—	34	8 <sup>b</sup>	—	
Admiralty Inlet, E Canada	April–June 1991	66	0	0	24	0	—	Furgal et al. (1996)
	April–June 1992	149	17	3	7	1	—	
	March–April 1993	22	0	0	0	0	—	
	1991–1993	—	26	3	25	1	0.02	

Barrow Strait, E Canada	combined 1975	156	15	3	—	—	—	Smith (1980) <sup>a</sup>
	1976	207	42	8	—	—	—	Hammill and Smith (1991)
	March–May 1984	174	18	2	1	0	0.06	
	March–May 1985	156	30	5	0	0	0.13	
	March–May 1986	232	28	7	2	0	0.48	
SE Baffin Island, E Canada	1978	17	12	0	—	—	—	Smith (1980) <sup>a</sup>
Kongsfjorden, Svalbard, Norway	1979	222	20	7	—	—	—	Lydersen and Gjertz (1986) <sup>d</sup>
	March–April 1984	90	14	1	21	7	—	

<sup>a</sup>Study focused only on polar bear predation. Area surveyed was not reported.

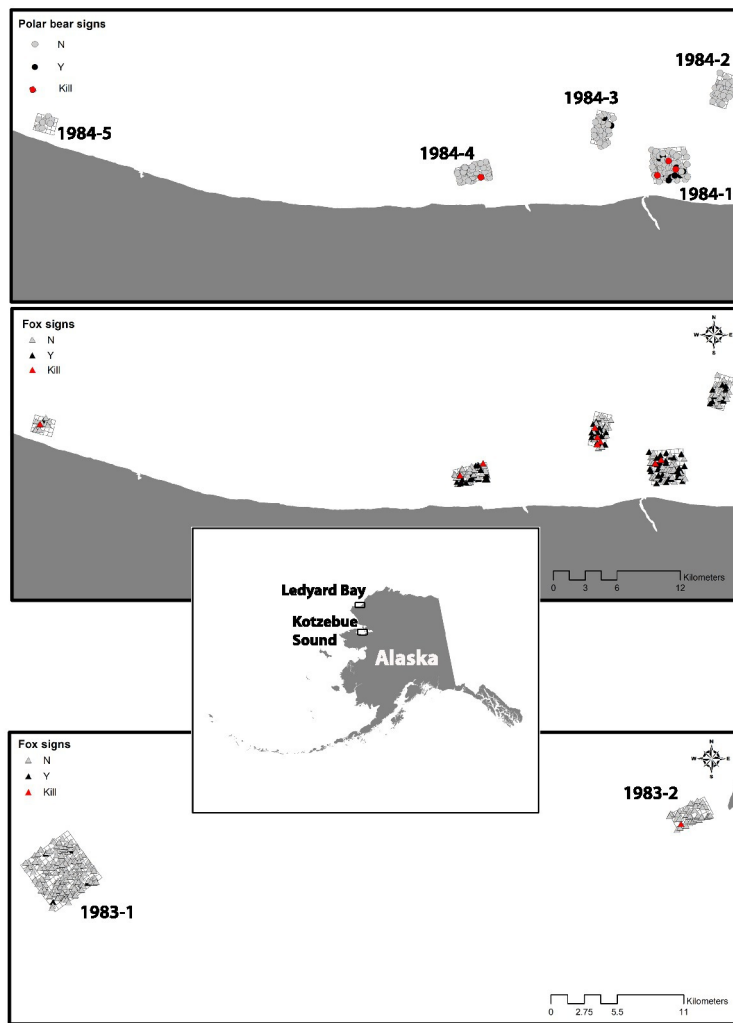
<sup>b</sup>Includes 17 “definite” and 13 “probable” ringed seal kills. All were pups.

<sup>c</sup>Study focused only on arctic fox predation. Area surveyed was not reported.

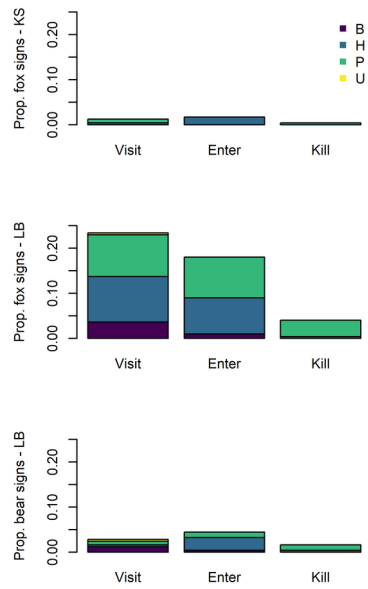
<sup>d</sup>Area surveyed was not reported.

**FIGURE 1** Study areas in Ledyard Bay (top and center panels) and Kotzebue Sound (bottom panel) in the Chukchi Sea, northwest Alaska. Ringed seal structures with signs of polar bear or fox predation or presence are shown in black, seal kills are shown in red, and those without signs of predators are shown in gray.

**FIGURE 2** Proportion of ringed seal structures (B = breathing hole; H = haul-out lair; P = pup lair; U = unclassified) that were visited, entered, or had a seal kill by arctic foxes in Kotzebue Sound (top), Ledyard Bay (middle), or by polar bears in Ledyard Bay (bottom).



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