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## RESEARCH ARTICLE

# Wolf density and predation patterns in the Canadian High Arctic

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## Abstract

The Arctic wolf (*Canis lupus arctos*) is a predator of muskoxen (*Ovibos moschatus*), Arctic hares (*Lepus arcticus*), and endangered Peary caribou (*Rangifer tarandus pearyi*) in the Canadian High Arctic. Although Arctic wolves potentially affect the dynamics of muskoxen and Peary caribou populations, knowledge about their abundance, distribution, and predation patterns is limited. Inuit and Inuvialuit communities value these species for sociocultural and subsistence reasons, and community members are concerned about how interactions among these species and their environment may change in a warming, unpredictable Arctic. We conducted a study from 2014–2018 of wolves in the rolling tundra of central Ellesmere Island (Fosheim Peninsula) and eastern Axel Heiberg Island. This area supported relatively high densities of muskoxen and Arctic hares, and previously supported Peary caribou, although caribou were mostly absent in the area during our study. We deployed global positioning system (GPS) radio-collars on 10 adult wolves in 6 packs on Ellesmere and Axel Heiberg islands to describe wolf density and predation patterns. Wolves were neither nomadic nor migratory; they remained on territories year-round, with summer densities of 2.5–8.0 adult wolves/1,000 km<sup>2</sup> and 3.7–10.4 wolves/1,000 km<sup>2</sup> including pups. Based on a ground search of 312 of 868 location clusters over a 340-day period, wolves in a focal study pack killed approximately 0.12 muskoxen/day, equivalent to a predation rate of 5.5–17.0% of the

estimated muskox population (older than 10 months old). This predation rate is likely sustainable given that calves and yearlings rather than reproductive adults comprised most documented kills, and that muskox populations can increase at rates up to 20%. The kill rate for this pack also implied a biomass intake deficit of 0.82–1.63 kg/wolf/day that could have been offset by each wolf consuming 115–228 Arctic hares annually. The decline of Peary caribou in the study area precluded any assessment of wolf predation influences on their population, but annual telemetry data confirming the year-round presence of a wolf–ungulate–hare system with relatively high wolf densities suggests that apparent competition could present a challenge to Peary caribou recovery efforts.

#### KEYWORDS

Arctic hare, Arctic wolf, *Canis lupus arctos*, muskox, *Ovibos moschatus*, Peary caribou, predation rate, *Rangifer tarandus pearyi*

The grey wolf (*Canis lupus*) is an integral part of predator–prey systems across its circumpolar range and of a model system for understanding the ecology of predator–prey interactions. The effects of wolves on prey populations and ecosystems have been well studied (Mech and Peterson 2003, Vucetich and Peterson 2004, Peterson et al. 2014, Wilmers and Schmitz 2016, Smith et al. 2020). These studies underscore the range of effects wolves can have depending on the system, as they are adaptable predators interacting with prey species that have their own highly evolved, effective defenses (Mech et al. 2015).

The interactions of Arctic wolves (*Canis lupus arctos*), Peary caribou (*Rangifer tarandus pearyi*), and muskoxen (*Ovibos moschatus*) in the Canadian Arctic Archipelago (CAA) represent a relatively simple predator–prey system. The CAA covers almost 1.5 million km<sup>2</sup> north of the Canadian mainland in Nunavut and the Northwest Territories, including >36,000 islands (Kaluskar et al. 2019). Although wolves and ungulates are arguably the most studied wildlife predator–prey system in the world, wolf–ungulate systems in the CAA remain poorly understood, a key knowledge gap considering that these systems are likely more exposed to the effects of climate change than any of the better-studied systems. According to Inuit *qaujimajatuqangit* (IQ; traditional knowledge and worldview), wolves affect muskox and caribou populations and these 2 ungulates affect each other, but the mechanisms are unknown (IQ reported in Taylor 2005, Johnson et al. 2016). Caribou, muskoxen, and wolves are important culturally and for subsistence of modern Inuit and Inuvialuit, and community members are concerned about how interactions among Peary caribou, muskoxen, and wolves may change in a warming, unpredictable Arctic (Johnson et al. 2016).

Muskoxen are the dominant ungulate across much of the circumpolar High Arctic based on population size and distribution. Dominant causes of change in muskox populations are likely a combination of interacting factors that vary across their circumpolar range (Cuyler et al. 2020), including nutritional stressors (Afema et al. 2017), predation (Reynolds et al. 2002, Arthur and Del Vecchio 2017), low genetic diversity (Laikre et al. 1997, Prewer et al. 2020), parasites and disease (Kutz et al. 2013, 2015; Ytrehus et al. 2015), and inclement weather (Forchhammer and Boertmann 1993, Miller 1998). In the CAA, muskoxen and Peary caribou are subject to periodic die-offs, caused by widespread starvation when freezing rain or rain-on-snow events prevent access to forage under thick ice layers (Miller et al. 1975, Miller and Gunn 2003, Miller and Barry 2009, Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2015). While muskox populations in the northern CAA appear stable or increasing (Anderson and Kingsley 2017, Cuyler et al. 2020,

Fredlund et al. 2019), there is significant uncertainty about how climate change will influence this species and what constitutes the range of natural variation for fluctuations in muskox abundance (Cuyler et al. 2020).

Peary caribou are a small (adult females 54 kg, adult males 66 kg; Thomas and Everson 1981), pale subspecies of caribou that almost exclusively occur in the CAA, moving across sea ice to access seasonal ranges. Although they cover long distances, Peary caribou do not undertake the long predictable migrations of barren-ground caribou (*R. t. groenlandicus*) on mainland Canada and Alaska, USA, nor do they aggregate in large herds (Taylor 2005, COSEWIC 2015). Their patchy, low-density distribution is similar to that of woodland caribou (*R. t. caribou*), suggesting a similar space away anti-predator strategy (Bergerud 1988, Seip 1992). Peary caribou are listed as threatened under Canada's Species at Risk Act with a population estimate of 13,200 adult caribou, well below historical levels but increasing from around 5,400 adult caribou in 1996 (COSEWIC 2015). There is little information on the role of wolf predation on muskox and Peary caribou persistence under present conditions, and even the most general proxies we can use to model potential predation effects, such as wolf density and seasonal presence, are not available for most of the CAA.

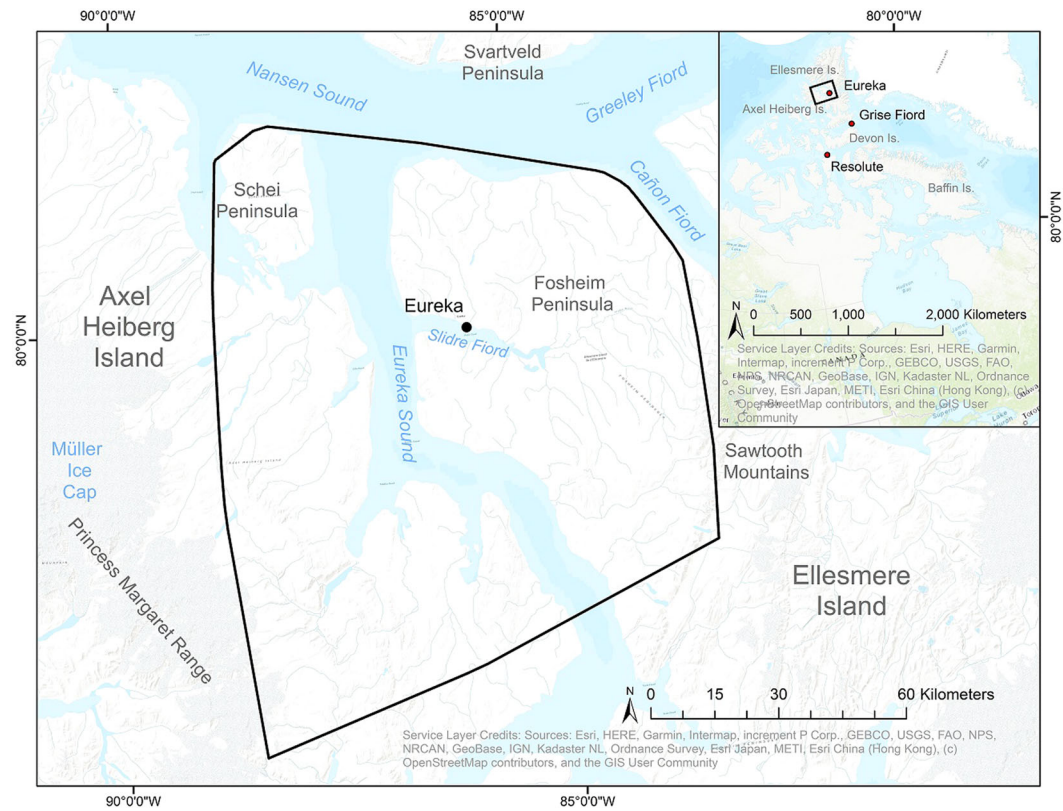
Arctic wolves are classified by COSEWIC as data deficient because of insufficient information on populations, trends, and diet (Van Zyll de Jong and Carbyn 1999). Most of what we know about Arctic wolves comes from incidental observations (Miller 1978, 1993; Miller and Reintjes 1995), behavioral observations of 1 pack at Eureka, Ellesmere Island (Mech 1988, 1995, 1997, 2004; Mech et al. 2025), studies of 1 global positioning system (GPS) radio-collared wolf in the same study area (Mech and Cluff 2011, Cluff and Mech 2023), and work on a recently re-established population in northern Greenland (Marquard-Petersen 1998, 2009). Although Inuit attitudes toward, and harvest of, Arctic wolves have been consistent over time, Western attitudes have changed dramatically. Arctic wolves were persecuted in the 1940s and 1950s, consistent with the prevailing Western attitudes towards predators at the time, which shifted to acceptance. People started habituating wolves at weather stations and military bases (Miller 1993). Changing attitudes, tighter regulations, and more oversight re-defined the wolf-human relationship at these outposts, such that food waste was incinerated and people were not permitted to feed wildlife. In the case of the Eureka weather station, wolves were still accustomed to people, providing a unique opportunity to document wolf behavior. This necessarily focused on the 1 pack that frequented the station and only during summer, so population-level questions remained unanswered.

We initiated this study to address basic knowledge gaps about wolf density, space use, and predation patterns required to make science-based recommendations for Peary caribou recovery, muskox management, and wolf status assessment in Nunavut's High Arctic Region. We investigated wolf density, whether wolves remained on territories in the study area year-round, wolf kill rates on each prey species, and predation rate on muskoxen (% of population killed by wolves annually). Lack of caribou in the study area during our study precluded investigation of wolf predation on caribou.

## STUDY AREA

Our study area, based on the locations of radio-collared wolves from 30 June 2014 to 30 June 2018, encompassed 16,505 km<sup>2</sup> of polar desert on Ellesmere Island's Fosheim Peninsula and the eastern slopes of Axel Heiberg Island, Nunavut, Canada, centered on approximately 80° north latitude and 85° west longitude (Figure 1). Infrastructure and logistics typical of most wolf-ungulate studies were severely limited in our study area. Axel Heiberg Island was uninhabited, and the only permanent year-round human presence on central Ellesmere Island was the Eureka weather station. The only roads in the study area, <20 km along Slidre Fiord, connected weather station infrastructure and the airstrip. The Inuit community of Grise Fiord, population 120, was 400 km south of Eureka. Hunters from Grise Fiord preferred to hunt on southern Ellesmere Island and Devon Island, so human harvest activities in the study area were negligible (Anderson 2015, Fredlund et al. 2019).

Ellesmere Island is dominated by the mountains and ice caps of the Arctic Cordillera, but the Fosheim Peninsula is predominantly rolling terrain with ridges up to 600 m above sea level (Figure 1). The Sawtooth Mountains form a



**FIGURE 1** Study area for this Arctic wolf predation study, Nunavut, Canada, June 2014–July 2018.

natural barrier to animal movement running southwest-northeast across the peninsula. Eastern Axel Heiberg Island slopes from the Müller Ice Cap and Princess Margaret Range (2,210 m) in the southwest to Nansen Sound in the northeast. Eureka Sound separates Axel Heiberg Island from the Fosheim Peninsula but, like other waterways in the region, remains frozen for most of the year and is not a barrier to wolf movement. The terrain north and east of Greeley Fiord, Cañon Fiord, and Nansen Sound is rugged and glaciated, and we saw limited movement of collared wolves across these waterways. The Fosheim Peninsula and eastern Axel Heiberg Island were relatively productive for the latitude, but the sparse, low-growing vegetation was mostly prostrate and semi-prostrate shrub and herb tundra, cryptogam barrens, and wet sedge meadows (Walker et al. 2005).

Climate in the study area was typified by a short snow-free period between June and September with sea ice present to some extent year-round. July was the warmest month (mean temperature = 6°C) and February was the coldest (mean temperature = −37°C). Eureka has experienced a 3.2°C increase in annual mean temperature since 1972, primarily over winter (Lesins et al. 2010). Average annual precipitation was 36.3 mm, mostly falling in July and August. Daylight fluctuated seasonally. The sun rose in late February and days lengthened until mid-April when the sun remained above the horizon 24 hours a day. Constant daylight persisted until the end of August when the sun again dipped below the horizon. Days shortened rapidly from August until late October, when the sun remained below the horizon for several months.

Muskoxen and Arctic hares (*Lepus arcticus*) were common in the study area. Peary caribou were uncommon around Eureka, but they were present at relatively high densities on Axel Heiberg Island in 2007 (Jenkins et al. 2011). When we initiated our project in 2014, we saw very few caribou or recent sign on reconnaissance flights. An aerial survey of Peary caribou and muskoxen on Axel Heiberg Island in April 2019 detected too few

Peary caribou to calculate an abundance estimate (Mallory et al. 2020). Despite the lack of Peary caribou in the study area, information on Arctic wolf ecology can help direct and prioritize research elsewhere in Peary caribou range. The only other terrestrial predators in the study area were Arctic foxes (*Vulpes lagopus*) and ermine (*Mustela erminea*). Polar bears (*Ursus maritimus*) were present along coastlines but were not a significant terrestrial predator.

## METHODS

### Wolf density

During June 2014–July 2017, we deployed 10 GPS radio-collars on 4 adult male and 6 adult female wolves representing 6 wolf packs using capture and handling methods consistent with Sikes et al. (2016). We immobilized wolves by helicopter darting or net-gunning and chemically immobilized them with Telazol™ (tiletamine-zolazepam) at 7 mg/kg. Once immobilized, we fitted wolves with radio-collars (Lotek Wireless, Newmarket, ON, Canada, and Vectronic Aerospace, Berlin, Germany). We programmed collars to collect 1 location every hour or every 2 hours and programmed remote drop-offs for 1 or 2 years post-deployment.

Most studies report pack counts for wolves during winter as recommended by Mech (1973), but without daylight or aircraft at Eureka during winter, we used summer pack counts instead. Mid-winter pack sizes and densities would likely fall between our summer minimum (adults only) and maximum (adults and pups) pack counts. We determined pack size each summer by observing active wolf dens for  $\geq 48$  hours, with  $>1$  visit in June or July to confirm counts. Because wolves often used the same den in subsequent years, we were able to determine pack size even when radio-collars failed. We did not consider an assumption of 10% lone wolves in addition to pack members (Fuller 1989) because it was not clear whether the proportion of lone wolves would be the same in our study area.

We calculated wolf density each summer as wolves/1,000 km<sup>2</sup>, where the number of wolves equaled the sum of pack counts (with and without pups), and area equaled the sum of the summer territory sizes (95% minimum convex polygon [MCP] for locations between 1 Jun–30 Sep) of packs counted that summer. We calculated MCPs using adehabitatHR (Calenge 2006) in R 4.3.3 (R Core Team 2024). If a collar failed during a given summer, we used the average summer territory size for that pack. For the 2 packs with  $>1$  collared wolf, we used the average MCP calculated for all collared wolves. We used the sum of MCP areas for all counted packs as the denominator in the density calculation because it allowed the area monitored each season to change with the packs that we were able to observe and count; using the overall study area as the denominator would underestimate wolf density, as we were not able to account for packs without reliable counts at dens. We also generated home ranges based on a dynamic Brownian bridge movement model (package move; Kranstauber et al. 2023) to visually examine intensity of use between seasons, years, and individuals. Although the MCPs we calculated for each pack in each season overlapped other pack seasonal MCPs, overlap between pack home ranges was minimal in any given season and year. There did not appear to be consistently unoccupied areas between packs in the study area.

Ungulate biomass has been used to predict regional wolf densities at lower latitudes (Fuller et al. 2003, Kuzyk and Hatter 2014, Mech and Barber-Meyer 2015). We used the Mech and Barber-Meyer (2015) equation  $y = 2.06 + 3.53x$ , where  $y$  is wolf density (wolves/1,000 km<sup>2</sup>) and  $x$  is ungulate biomass index (UBI). We estimated UBI as the sum across ungulate species of their density (i.e.,  $N/\text{km}^2$ ) multiplied by a prey-specific coefficient, which we set at 2.5 for muskoxen, based on body size relative to those used in earlier regressions: UBI = 1 for sheep (bighorn [*Ovis canadensis*] and Dall's [*O. dalli dalli*]), mountain goats (*Oreamnos americanus*), and deer (*Odocoileus* spp.); 2 for caribou; and 3 for elk (*Cervus canadensis*). The Government of Nunavut conducted an aerial survey for Peary caribou and muskoxen on central Ellesmere Island in March 2017, which provided an estimate of 4,954 muskoxen (95% CI = 3,461–7,091 muskoxen) in the 11,543-km<sup>2</sup> Fosheim Peninsula stratum (0.42 muskoxen/km<sup>2</sup>, 95% CI = 0.30–0.61 muskoxen/km<sup>2</sup>; Fredlund et al. 2019), an area overlapping the study area. We assumed the muskox density on eastern Axel Heiberg Island was the same as on the Fosheim Peninsula, as it is more



topographically and vegetatively similar to the Fosheim than to the remainder of the island. Peary caribou density was negligible, so we assumed a density of 0 Peary caribou/km<sup>2</sup> (Fredlund et al. 2019, Mallory et al. 2020).

## Kill site characterization

We identified potential kill sites by using a location-clustering algorithm (Knopff et al. 2009), which assigned nearby collar locations to a cluster, with start and end times defined as the first and last points in the cluster, and the cluster centroid calculated from all locations in the cluster. We defined location clusters as  $\geq 2$  collar locations (i.e.,  $>1$  or  $>2$  hr apart) from an individual wolf within 50 m and investigated a subset of location clusters with thorough ground searches.

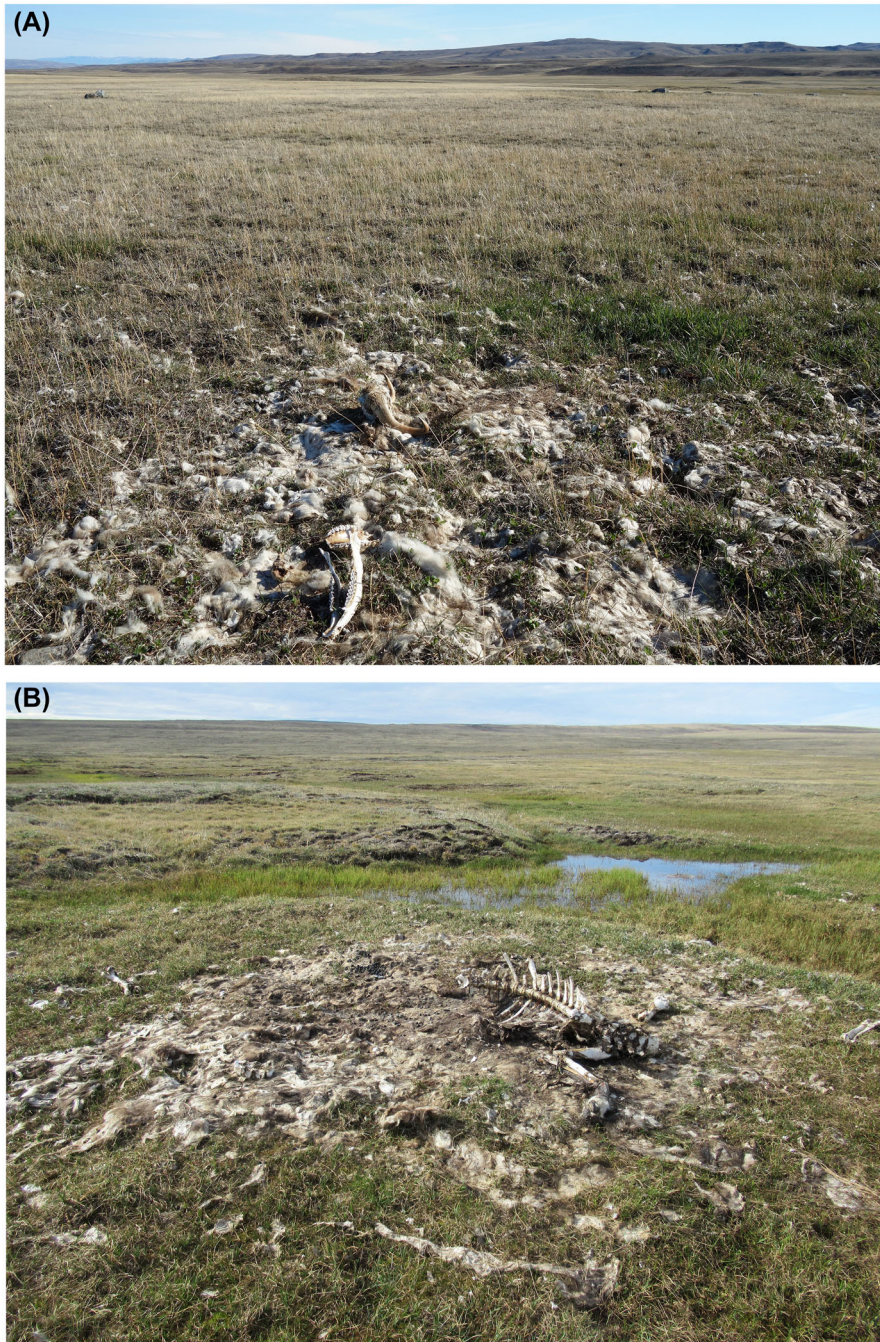
We identified muskox kill sites by a mat of hair, rumen contents, and bones. We classified carcasses to age and sex based on tooth eruption and horn morphology and collected an incisor for cementum annuli aging (Matson's Laboratory, Manhattan, MT, USA) when possible. We examined marrow from intact long bones as a qualitative indication of body condition (white waxy marrow with high fat content or red gelatinous marrow with low fat content; Mech 2008). Marrow fat is the last fat store depleted, so presence of marrow fat does not necessarily indicate an animal in good condition, but lack of marrow fat does indicate poor condition (Mech and DelGuidice 1985). We assumed thoroughly consumed, disarticulated carcasses were kills rather than scavenges (Figure 2A), although some scavenged carcasses may have had similar consumption as kills. We distinguished scavenged carcasses by the presence of rumen contents in place in the ribcage and articulated bones, particularly limbs (Figure 2B). There were no other large carnivores in the study area that prey on muskoxen; any scavenged carcasses would have been from non-predation mortality. The cluster algorithm was meant to identify potential large animal kill sites, but we were also able to identify kills of Arctic hares by mats of fur and presence of occasional bones and cecum contents.

Given logistical challenges of our study area due to inclement weather, restricted seasonal daylight, and accessibility, we were limited in how many clusters we could investigate. As such, we employed an overall opportunistic approach involving air and ground investigation of clusters from all packs from 2014–2018, including investigation of 185 out of 1,087 clusters determined for 3 collared wolves in the Axel Heiberg pack by hiking 100 km between 5–9 July 2016. This was followed by a focused investigation of clusters from the Eureka pack between 16 July 2017 and 21 June 2018. The opportunistic searches allowed us to search as many clusters as possible to maximize detection of kills, while the targeted investigation provided data for estimating kill and predation rates for 1 pack. We prioritized clusters with more locations, as the number of locations in a cluster was one of the best predictors of wolf kill sites (Zimmerman et al. 2007, Irvine et al. 2022).

## Kill rates and predation rates

We selected a focal pack and period for which to visit all likely kill sites (clusters with  $\geq 10$  location points) and some clusters with  $<10$  location points. Searching long-duration clusters (i.e., clusters with  $\geq 10$  locations) was more likely to provide information on large ungulate kills at the expense of determining the outcome of all clusters over a given period, whereas our inclusion of some clusters with  $<10$  location points allowed us to assess these potential biases. We covered 327 km on foot between 30 June and 13 July 2018 to search 312 of 868 location clusters generated by 1 collared wolf (W448) in the Eureka pack over 340 days (16 Jul 2017 to 21 Jun 2018).

There is the possibility of false negatives where observers do not find evidence of a carcass when one is present. We expected a false negative rate lower than the 4% false negative rate determined for cougar (*Puma concolor*) kills investigated 4–60 days after the kill in Colorado, USA (Blecha and Aldredge 2015), as our study area lacked obscuring vegetation cover, had few scavengers to remove or consume carcass parts, and had a climate that allowed carcass remains to persist longer than in temperate environments. Although our cluster investigations



**FIGURE 2** Muskox remains at wolf location clusters investigated during an Arctic wolf predation study on Ellesmere and Axel Heiberg Islands, Nunavut, Canada, June 2014–July 2018, to determine prey species and demographics: A) adult female muskox killed by the Axel Heiberg pack (note completely disarticulated and scattered carcass remains) on 26 December 2014 and investigated by M. Anderson and E. Akeeagok on 9 July 2016 (image by M. Anderson); and B) adult male muskox scavenged by the Eureka pack (note rumen contents in place within rib cage, articulated limbs) on 2 August 2017 and investigated on 5 July 2018 by M. Anderson and D. MacNulty (image by M. Anderson).



necessarily occurred with a search delay of weeks to months, carcass remains were easily detected (Figure 2); bone and antler can persist in this landscape for centuries (Mech and Packard 1990).

To assess the likelihood of missed kill sites during ground investigations, we compared the number of hourly location fixes at all clusters we investigated where we found and did not find muskox remains using a single-factor random analysis of variance (ANOVA) test with  $\alpha = 0.05$  in program R 4.3.3 (R Core Team 2024). We then fit a logistic regression to the clusters we visited during the 2018 search to determine if the number of locations in the cluster could be used to predict the probability that the cluster represented a muskox kill. Based on this analysis, we estimated the number of kills that we missed.

We estimated wolf predation rates on muskoxen (proportion of muskox population killed annually by wolves) using the kill rates (number of muskoxen killed annually by wolves) derived for the Eureka pack. We calculated an annual kill rate for the Eureka pack by adding all kills detected to the estimated number of missed kills. We then determined the predation rate for the Eureka pack as the proportion of the prey population removed by the predator (Vucetich et al. 2011) using the density estimate of 0.429 muskoxen/km<sup>2</sup> from the Fosheim Peninsula stratum on the 2017 Government of Nunavut survey (95% CI = 0.300–0.614 muskoxen/km<sup>2</sup>; Fredlund et al. 2019) applied over the 8,750-km<sup>2</sup> study area (excluding waterways). This provided a population estimate of 3,754 muskoxen (95% CI = 2,625–5,373 muskoxen). We used the estimated kill rate from the Eureka pack and our estimates of wolf density and muskox density to approximate the total wolf predation rate for the study area. This procedure assumed that the Eureka pack kill rate was representative of other packs, that the collared wolf clusters were representative of Eureka pack activity, and that muskox density was consistent during the study.

Using our estimate of the Eureka pack's kill rate, we estimated the amount of muskox biomass acquired by assigning body mass estimates based on the age and sex of muskoxen killed and excluding hair, bones, and ingesta. Ingesta content varied throughout the year, comprising 20–28% of muskoxen live mass in other populations (Staal and Thing 1991; Adamczewski et al. 1995, 2009). Carcass compositions of muskoxen indicate 4.0–4.5% of live mass is hair and about 15% is bone (Adamczewski et al. 1995). We therefore considered the edible biomass of a muskox carcass as 56% of its live total mass (total live mass minus 25% ingesta, 4% hair, and 15% bone). We considered mass reported in the literature for adult muskoxen in North America (Table 1). Muskox calves and yearlings grow rapidly, so we estimated body mass for males and females by month from 50–100 kg (Peltier and Barboza 2003). We considered neonates as 10 kg of edible biomass for the few neonate kills that we detected (others were likely undetected but contributed little to biomass intake). Scavengers, especially ravens (*Corvus corax*), were less abundant in our study area than in systems where the effect of scavenging has been investigated, so we did not account for any loss of biomass to scavengers. We used the biomass equivalent of female muskoxen for the estimated missed muskox kills, acknowledging that these could have represented calves, yearlings, males, or multiple muskoxen. We considered well-used wolf-scavenged carcasses to be equivalent in biomass intake to a kill (Metz et al. 2011), but we did not include scavenged carcasses in calculations of the kill rate or predation rate.

To approximate the kill rate of Arctic hares, we considered whether biomass intake from muskoxen (including scavenged muskoxen) was sufficient to support the Eureka wolves or whether there was a deficit to be filled from other sources. We assumed that an Arctic wolf would require the same 3.25 kg/wolf/day as a 35-kg temperate wolf (Peterson and Ciucci 2003). Arctic hares were the only other significant prey species (Mech 2005, 2007; Mech et al. 2015). We assumed adult hares (4 kg with 65% live mass [2.6 kg] as edible biomass; Jedrzejewski et al. 2002) made up the deficit, but wolves also prey on juvenile hares (Mech et al. 2015).

## RESULTS

### Wolf density

The 10 collared wolves remained on territories year-round during 2014–2018 (Table 2; Figure 3), except for occasional off-territory movements and 2 wolves that dispersed. A collared non-breeding male in the Eureka pack

**TABLE 1** Body mass of muskoxen reported for North America and Greenland and used to estimate biomass consumed by the Eureka pack of Arctic wolves on Ellesmere Island, 2018.

| Age and sex of muskox    | Total body mass (kg) | Inedible mass (ingesta, bone, hair) (kg) | Estimated edible mass (kg) | Reference   |
|--------------------------|----------------------|--|----------------------------|---|
| Adult male               | 280                  | 123.2                                    | 155                        | West Greenland: $321 \pm 11$ (SD) kg in summer and $290 \pm 32$ kg winter (Olesen et al. 1994); East Greenland: $286 \pm 30$ kg in summer and $220 \pm 41$ kg in winter (Olesen et al. 1994); Alaska, USA: 273–364 kg (Alaska Department of Fish and Game [ADF&G] 2010); Banks Island, Northwest Territories, Canada: 277 kg in May (Latour 1987) |
| Adult female             | 200                  | 88                                       | 90                         | 25% smaller than males (Klein 2000); Banks Island: 167 kg for captive muskox (Chaplin and Stevens 1989); Victoria Island, Northwest Territories: 116–176 kg ingesta-free weight between May and Sep (Adamczewski et al. 2009); Alaska: 182–257 kg (ADF&G 2010)  |
| Calf, Oct                | 50                   | 20                                       | 30                         | Estimated from Peltier and Barboza (2003)   |
| Calf, Nov–Dec            | 60                   | 25                                       | 35                         | Estimated from Peltier and Barboza (2003)   |
| Calf, Jan–Mar            | 70                   | 30                                       | 40                         | Estimated from Peltier and Barboza (2003)   |
| Calf, Apr–May            | 80                   | 35                                       | 45                         | Estimated from Peltier and Barboza (2003)   |
| Yearling male, Jun–Aug   | 90                   | 40                                       | 50                         | Estimated from Peltier and Barboza (2003)   |
| Yearling female, Jun–Aug | 80                   | 35                                       | 45                         | Estimated from Peltier and Barboza (2003)   |
| Yearling male, Sep       | 100                  | 44                                       | 55                         | Estimated from Peltier and Barboza (2003)   |
| Yearling female, Sep     | 90                   | 40                                       | 50                         | Estimated from Peltier and Barboza (2003)   |

(W444) dispersed to Axel Heiberg Island and became the breeding male in the Axel Heiberg pack. A collared subordinate female in the Axel Heiberg pack (W445) dispersed south to Devon Island (600 km straight-line distance) on the shore of ice-free Lancaster Sound.

Pack size varied from 2 adults and no pups to 10 adults and 11 pups, with a mean pack size of  $4.9 \pm 0.6$  (SE) adult wolves ( $n = 22$ ), or  $8.3 \pm 1.0$  wolves including pups ( $n = 23$ ). Summer 95% MCPs ranged from 400–2,130 km<sup>2</sup> ( $\bar{x} = 1,131$  km<sup>2</sup>, SE = 633,  $n = 6$  packs). Based on summer pack counts in our study area and summer territory sizes (Table 3), we estimated annual summer densities of 4.7 adult wolves/1,000 km<sup>2</sup> (range = 2.5–8.0 adult

**TABLE 2** Radio-collared wolves, sex (male [M], female [F]), age, pack affiliations, and collar performance for Arctic wolf packs monitored on Ellesmere and Axel Heiberg islands in Nunavut, Canada, from 2014–2018.

| Wolf | Sex | Age at capture | Pack                 | Collar type and schedule (number of locations) | Collar duration (days) and deployment dates | Collar fate                        |
|------|-----|----------------|----------------------|--|---|------------------------------------|
| W440 | M   | 2 yr           | Axel Heiberg         | Lotek 1-hr fixes (9,204)                       | 38415 Jul 2014–3 Aug 2015                   | Collar likely dropped <sup>a</sup> |
| W441 | F   | 2 yr           | Cañon Fiord          | Lotek 1-hr fixes (3,888)                       | 16430 Jun 2014–10 Dec 2014                  | Collar failure <sup>a</sup>        |
| W442 | F   | Adult          | Wolf Valley          | Lotek 1-hr fixes (531)                         | 236 Sep 2014–28 Sep 2014                    | Collar failure <sup>a</sup>        |
| W443 | M   | Adult          | Hot Weather Creek    | Lotek 1-hr fixes (17,400)                      | 7256 Sep 2014–31 Aug 2016                   | Collar failure <sup>a</sup>        |
| W444 | M   | Adult          | Eureka, Axel Heiberg | Vectronic 1-hr fixes (9,350)                   | 5883 Jun 2015–11 Jan 2017                   | Collar failure <sup>a</sup>        |
| W445 | F   | Adult          | Axel Heiberg         | Vectronic 2-hr and 1-hr fixes (7,874)          | 3925 Jun 2015–1 Jul 2016                    | Collar likely dropped <sup>a</sup> |
| W446 | F   | Adult          | Mt Lockwood          | Vectronic 1-hr fixes (4,185)                   | 1766 Jul 2016–29 Dec 2016                   | Collar failure <sup>a</sup>        |
| W447 | F   | 2 yr           | Eureka               | Vectronic 1-hr fixes (4,426)                   | 1876 Jul 2016–9 Jan 2017                    | Mortality, carcass consumed        |
| W448 | F   | ~6 yr          | Eureka               | Lotek 1-hr fixes (7,948)                       | 35015 Jul 2017–30 Jun 2018                  | Collar failure <sup>a</sup>        |
| W449 | M   | ~3 yr          | Eureka               | Lotek 1-hr fixes (3,710)                       | 23518 Jul 2017–10 Mar 2018                  | Collar failure <sup>a</sup>        |

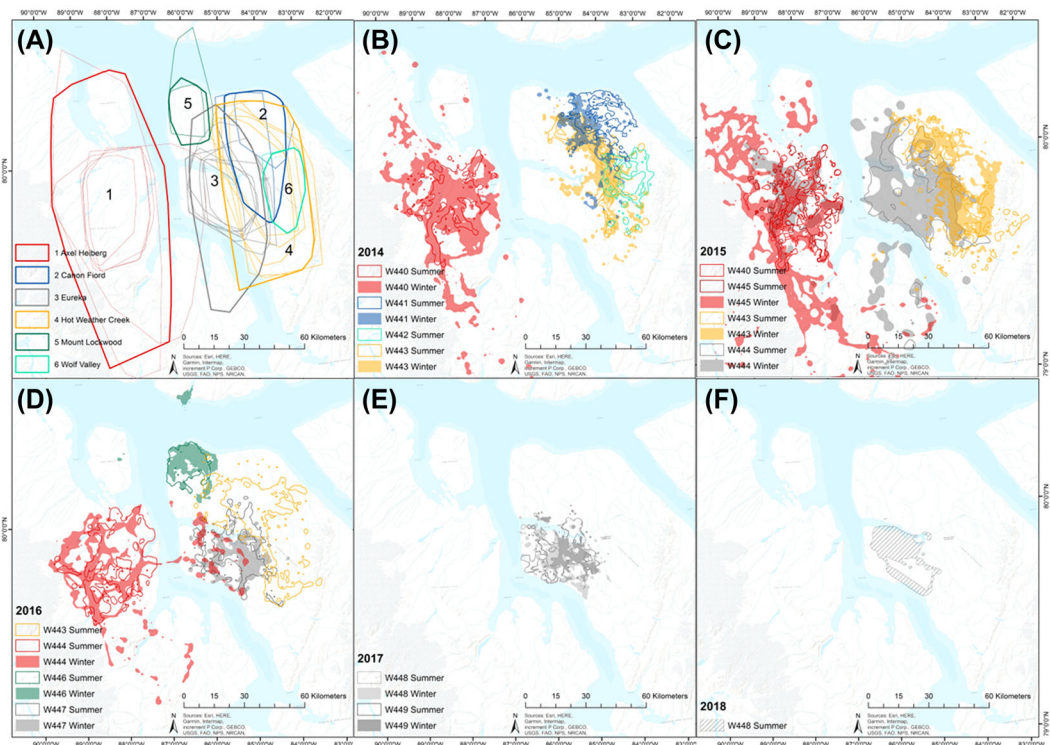
<sup>a</sup>Collar not retrieved.

wolves/1,000 km<sup>2</sup> for 2014–2018) and 7.6 wolves/1,000 km<sup>2</sup> including pups (range = 3.7–10.4 wolves/1,000 km<sup>2</sup> for 2014–2018, Table 4).

We estimated the UBI in the study area, based on the muskox densities estimated by Fredlund et al. (2019) in March 2017 (1.07 muskoxen/km<sup>2</sup>, 95% CI = 0.75–1.54/km<sup>2</sup>). This value predicted 5.8 wolves/1,000 km<sup>2</sup> (95% CI = 4.7–7.5 wolves/1,000 km<sup>2</sup>) according to Mech and Barber-Meyer's (2015) biomass model. Predicted densities overlapped the range of observed annual summer densities and the mean densities over the study. In some years, observed adult-only summer densities were lower than predicted and densities including pups were higher than predicted, but this would be expected for predictions of mid-winter wolf density (Table 4).

### Kill site characterization

From 2014–2018 we investigated 550 location clusters on the ground and 42 from the air from all packs and identified the remains of 85 muskox carcasses (83 kills and 2 scavenges), 59 hare kills, 1 wolf carcass, and 1 ringed seal (*Pusa hispida*) on sea ice (likely scavenged). Additional clusters appeared to be associated with lemming (*Dicrostonyx groenlandicus*) activity, Arctic fox dens, and molting brant (*Branta bernicla*) at wetlands. We did not find any caribou kills during cluster investigations, although we found several weathered shed antlers demonstrating past caribou presence in the study area.



**FIGURE 3** Home ranges for 10 Arctic wolves in 6 packs on Ellesmere and Axel Heiberg Islands, Nunavut, Canada, by season (winter, summer) and year during June 2014–July 2018. Polygons in frame A indicate the 95% minimum convex polygon territories for wolf packs with thin lines for each wolf and season and bold lines for locations from all wolves and years. Polygons in frames B through F indicate home ranges from the 95% dynamic Brownian bridge movement model for winter (shaded) and summer (outlined) for wolves monitored each year.

Based on the July 2017–June 2018 Eureka wolf clusters, residency was longer at muskox carcasses (kills and scavenges,  $\bar{x}$  = 30.9 hourly location fixes,  $SD$  = 19.7,  $n$  = 41 clusters; Figure 4) than at clusters where we found no evidence of a carcass ( $\bar{x}$  = 7.2 hourly location fixes,  $SD$  = 9.0,  $n$  = 213 clusters;  $P$  < 0.001). We found the remains of  $\geq 1$  Arctic hare at clusters ( $\bar{x}$  = 7.6 hourly location fixes,  $SD$  = 4.2,  $n$  = 47 clusters; Figure 4) that could not be distinguished from clusters where we found no carcass ( $P$  = 0.86). We visited a representative sample of 307 clusters during the intensive 2018 search based on number of locations per cluster (Figure 5). We found hare remains at 15% of the investigated clusters in 2018. Almost half (43.6%) of the 39 muskox kills detected during the systematic search in July 2018 were calves ( $n$  = 15, including 3 neonates) and yearlings ( $n$  = 3). The remaining muskox kills were adults (7 males, 13 females, 1 unknown) and both scavenges were adult males. Wolf-killed adult muskoxen from all kill sites in 2014–2018 were 4–10 years old ( $\bar{x}$  = 5.7 years,  $SE$  = 1.9,  $n$  = 46 adult muskoxen) based on cementum annuli aging, but some muskoxen were aged younger using this method than based on observed horn boss development and tooth wear. Of the 16 kills (all sex and age classes) where intact long bones were present during the 2018 search, 87.5% had waxy white marrow and 12.5% had red gelatinous marrow indicative of poor condition.

### Kill rates and predation rates

Our systematic search revealed 39 muskox kills for the Eureka pack between Jul 2017–Jun 2018, when the Eureka pack included  $\geq 4$  adult wolves (pack counts of 4 adult wolves and 3 pups in Jul 2017, and 4 adult wolves in



**TABLE 3** Pack sizes for Arctic wolf packs (number of adults with number of pups in parentheses; unk for active den with unknown number of pups) and summer territory size (95% minimum convex polygon [MCP]; km<sup>2</sup>) monitored at dens on Ellesmere and Axel Heiberg islands in Nunavut, Canada, from 2014–2018. Bay Fiord and Vesle Fiord packs lived south of our study area and were never collared; Rock Den had uncertain pack affiliation and was not collared.

| Wolf pack         |           | 2014               | 2015                 | 2016    | 2017                 | 2018  | Mean <sup>a</sup> (±SE) |
|-------------------|-----------|--------------------|----------------------|---------|----------------------|-------|-------------------------|
| Eureka            | Pack size | 15–16 <sup>b</sup> | 13 (3)               | 10 (11) | 4 (3)                | 4 (0) | 7.8 ± 2.3               |
|                   | 95% MCP   |                    | 1,652.2              | 1,429.0 | 1,134.9 <sup>c</sup> |       | 1,192.6                 |
| Axel Heiberg      | Pack size | 7 (9)              | 9 (unk)              | 6 (6)   | 6 (unk)              |       | 7.0 ± 0.7               |
|                   | 95% MCP   | 1,182.4            | 1,679.9 <sup>c</sup> | 1,664.3 |                      |       | 1,551.6                 |
| Hot Weather Creek | Pack size | 2 (0)              |                      | 2 (5)   | 2 (3)                |       | 2.0 ± 0.0               |
|                   | 95% MCP   | 1,436.1            | 2,669.7              | 2,284.9 |                      |       | 2,130.2                 |
| Cañon Fiord       | Pack size | 6 (3)              |                      | 4 (unk) |                      | 6 (4) | 5.3 ± 0.7               |
|                   | 95% MCP   | 822.6              |                      |         |                      |       | 822.6                   |
| Mount Lockwood    | Pack size | 5 (3)              |                      | 2 (1)   |                      |       | 3.5 ± 1.5               |
|                   | 95% MCP   |                    |                      | 400.0   |                      |       | 400.0                   |
| Wolf Valley       | Pack size | 4 (4)              |                      |         |                      |       | 4.0                     |
|                   | 95% MCP   | 687.8              |                      |         |                      |       | 687.8                   |
| Rock Den          | Pack size |                    |                      |         | 2 (5)                |       | 2.0                     |
| Vesle Fiord       | Pack size | 3 (3)              | 5 (unk)              |         |                      | 4 (2) | 4.0 ± 0.6               |
| Bay Fiord         | Pack size | 2 (3)              |                      |         |                      |       | 2.0                     |

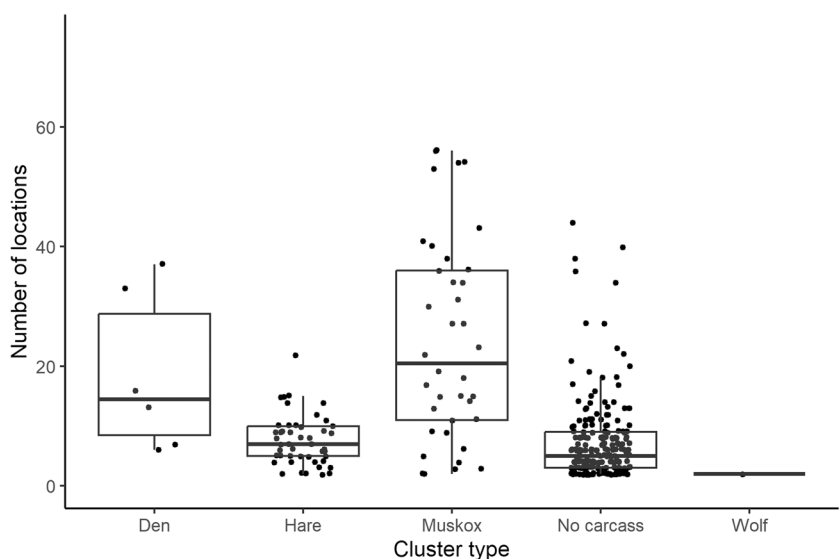
<sup>a</sup>Mean pack size equals mean number of adults.

<sup>b</sup>Based on observations at Eureka but not classified as adults and pups; not included in calculation of mean number of adults per pack.

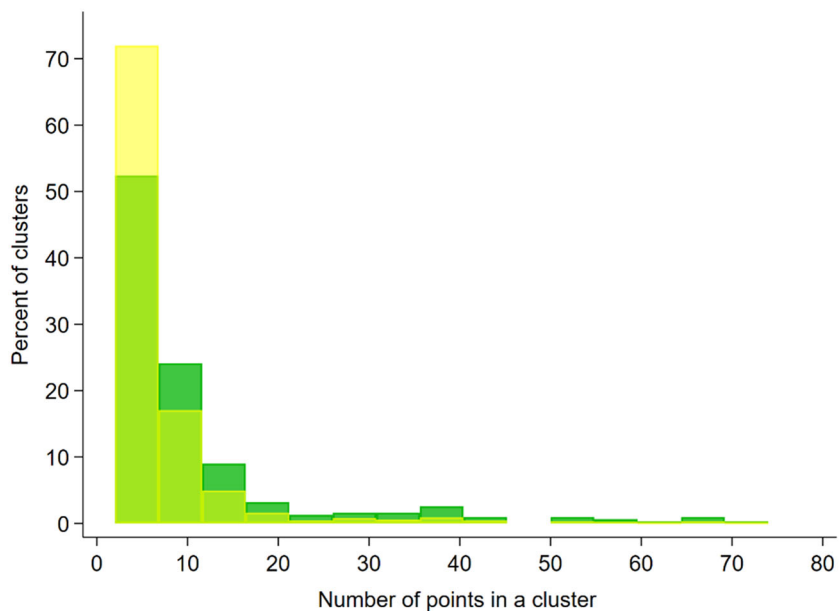
<sup>c</sup>Average MCP size of 2 collared wolves (both individual MCPs used to calculate overall average size, not the average value for the year).

**TABLE 4** Annual summer density of Arctic wolves calculated from counts of adult wolves and pups at dens and average 95% minimum convex polygon (MCP) summer territories for 6 radio-collared packs on Ellesmere and Axel Heiberg islands, Nunavut, Canada, 2014–2018.

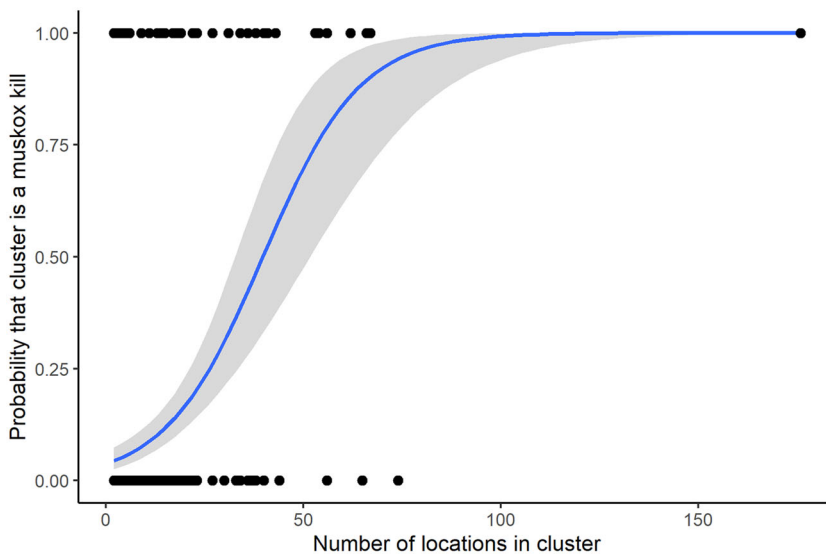
| Year       | MCP area (km <sup>2</sup> ) | Number of adult wolves | Number of adults and pups | Density of adults (wolves/1,000 km <sup>2</sup> ) | Density including pups (wolves/1,000 km <sup>2</sup> ) |
|------------|-----------------------------|------------------------|---------------------------|---|--|
| 2014       | 5,592                       | 24                     | 58                        | 4.3   | 10.4   |
| 2015       | 2,744                       | 22                     | 25                        | 8.0   | 9.1  |
| 2016       | 6,097                       | 24                     | 47                        | 3.9   | 7.7  |
| 2017       | 4,875                       | 12                     | 18                        | 2.5   | 3.7  |
| 2018       | 2,015                       | 10                     | 14                        | 5.0   | 6.9  |
| Mean (±SE) |                             |                        |                           | 4.7 ± 0.9   | 7.6 ± 1.1  |



**FIGURE 4** The number of hourly location fixes at hare kills, muskox kills, 1 wolf kill, den sites, and sites with no carcass present for location clusters of wolf W448 in the Eureka pack (Nunavut, Canada) from July 2017–June 2018 (boxplot with lower and upper bounds of the box are first and third quartiles, median at horizontal line, whiskers are 1.5× interquartile range and points beyond the whiskers are considered outliers; one muskox kill with 150 location points excluded from the plot for scale). Muskox kills were associated with location clusters with significantly more locations than clusters where we found hare remains. Clusters where we found hare remains had similar numbers of locations to clusters with no evidence of a carcass.



**FIGURE 5** Histogram showing the frequency distributions of location clusters investigated in 2018 (green; excluding 1 with 176 locations) and all clusters (yellow; light green represents overlap) of wolf W448 in the Eureka pack (Nunavut, Canada), July 2017–June 2018.



**FIGURE 6** Probability that a location cluster was associated with a muskox kill based on the number of locations in the cluster for wolf W448 in the Eureka pack (Nunavut, Canada) from July 2017–June 2018. Blue line and associated shaded area (95% CI) represent fitted values from a logistic regression. The probability of a muskox kill increased with the number of locations in the cluster, with 40 locations having a 50% probability of representing a muskox kill.

Jan 2018). The number of locations in a cluster was a significant ( $\beta = 0.0815$ ,  $SE = 0.0131$ ,  $P < 0.001$ ) predictor of the probability that the cluster represented a muskox kill; clusters with  $>40$  hourly locations had a  $\geq 50\%$  probability of representing a kill (Figure 6). Clusters with  $<10$  hourly locations had a  $\leq 8\%$  probability of representing a kill. We considered half of the unvisited clusters with  $>40$  locations to be missed muskox kills, but as there was only 1 unvisited cluster meeting this definition, we arbitrarily classified it as a missed kill. We excluded scavenged muskoxen from estimations of kill and predation rates because wolves were not the proximate cause of death. Based on the 39 known and 1 missed kill, the Eureka pack killed 40 muskoxen in 340 days, 0.12 muskoxen/day, or 1 muskox every 8.5 days. The average distance between consecutive known kills was 9.3 km ( $SE = 7.7$  km,  $n = 35$ ; 4 clusters had  $>1$  muskox killed). Including the 2 scavenged muskoxen and 1 predicted missed kill, we estimated that the wolves consumed 3,310 kg of edible muskox biomass, or 9.7 kg/day. Only 2 of the muskox kills we considered were from before September 2017, when most clusters seemed to be associated with hare kills, so most of these kills represent biomass obtained when pups were large and traveling with the pack, and we considered them metabolically equivalent to adults. The pack likely did not have pups in summer 2018, as none of the pack's known den sites were occupied. Assuming a pack of 6 wolves, biomass intake was 1.62 kg/wolf/day. If the pack included only 4 wolves, biomass intake was 2.43 kg/wolf/day, still below the 3.25 kg/wolf/day required by wild wolves. To make up for a deficit of 0.82–1.63 kg/wolf/day, the Eureka pack would have to consume the equivalent of 115–228 adult hares/wolf annually, based on a pack size of 4–6 wolves.

With our higher estimate of mean wolf density of 7.6 wolves/1,000 km<sup>2</sup> and the muskox density estimate based on Fredlund et al. (2019), 429 muskoxen/1,000 km<sup>2</sup> (95% CI = 300–614 muskoxen/1,000 km<sup>2</sup>), we would expect annual losses to wolf predation of 12.7% (95% CI = 8.9–18.1%) of the muskox population in the study area if the Eureka pack size was 6 wolves or 19.0% (95% CI = 13.2–27.2%) if the Eureka pack size was 4 wolves. The muskox abundance was based on a survey conducted in March and did not include any calves that died before reaching 10 months old. If we instead considered only muskoxen  $\geq 10$  months old that were killed by the Eureka pack, the annual losses were estimated at 7.9% (95% CI = 5.5–11.3%; 6 wolves) or 11.9% (95% CI = 8.3–17.0%; 4

wolves) of the muskox population in the study area. The predation rate reflected the maximum wolf densities estimated here (i.e., adults and pups) so actual predation rates were likely lower.

## DISCUSSION

Our objective was to assess factors influencing wolf predation on their dominant prey, muskoxen, including wolf density, prey selection, and predation rates. Prior to this work, it was unknown whether High Arctic wolves remained territorial year-round, migrated seasonally (Walton et al. 2001), or were nomadic when not denning. Our data showed that resident packs maintained year-round territories, as they do in most regions, at densities of about 4.7 adult wolves/1,000 km<sup>2</sup> (7.6 wolves/1,000 km<sup>2</sup> including pups). Thus, predation occurred year-round, exerting greater impact on muskox populations than if wolves were only present seasonally. We estimated an annual wolf predation rate of 5.5–17.0% on muskoxen >10 months old, depending on pack size. Because Arctic hares comprised a substantial portion of the wolf diet, their availability could affect wolf predation rate on muskoxen.

Our estimates of wolf density and average pack size were higher than those reported elsewhere in the High Arctic (Riewe 1975, Miller and Reintjes 1995, Marquard-Petersen 2009). Several factors could explain this discrepancy. One possibility is that our study area was relatively productive with a higher prey density. Additionally, the limited temporal scope of our study might have influenced the results, as pack dynamics could change dramatically because of severe stochastic weather causing large-scale ungulate die-offs (COSEWIC 2015, Cuyler et al. 2020). Previous observations of wolf pack sizes in the CAA relied on incidental summer reports when packs are less cohesive (Miller and Reintjes 1995, Demma and Mech 2009), potentially leading to undercounts. Furthermore, most wolf population density surveys have been conducted in winter, whereas our estimate was for summer. Wolf density estimates based only on adult wolves are likely similar to or slightly lower than those observed in mid-winter populations.

Young muskoxen were more likely killed by wolves than were adults (Mech 2010), comprising nearly half of wolf-killed muskoxen, despite late-winter calves accounting for only 13–22% of the population (Jenkins et al. 2011, Anderson 2014, Anderson and Kingsley 2017). This accords with other wolf–ungulate systems where prime-aged animals are generally least vulnerable (Huggard 1993, Mech et al. 2015, Boertje et al. 2020, Hoy et al. 2021). Although we did not attempt to estimate wolf predation rates on neonate muskoxen, we did find several neonate kills. The defensive stand-off behavior of muskoxen may have extended the time wolves spent at sites, resulting in larger location clusters than we would expect based on the handling time of a neonate carcass. While underestimating neonate kills would underestimate overall muskox predation rate, any calves that died before late winter were also not enumerated on surveys and not included in our muskox abundance estimates.

Our estimated predation rate on muskoxen, approximately 10%, was consistent with wolf predation rates on ungulates observed in other systems (Jędrzejewski et al. 2002, Gazzola et al. 2007, Vucetich et al. 2011). Prey populations, such as moose (*Alces alces*) on Isle Royale, Michigan, USA, have declined when predation rates exceeded 10% (Peterson et al. 2014). Our maximum predation-rate estimate (19%) is higher than those for wolf populations in less extreme environments. While muskox populations can grow by up to 20% annually in expanding populations (Spencer and Lesink 1970, Anderson 2016, Hansen et al. 2018), the exact population trajectory of our study's muskoxen was unknown, though it appeared stable from 2007 to 2017 (Jenkins et al. 2011, Fredlund et al. 2019).

Our estimates of kill and predation rates were based on data from a single individual in 1 pack over 1 year, which introduces several limitations. We may have missed some muskox kills if the collared wolf was not present at the kills (Mech 2011). A model predicting the attendance of individual pack members at kills predicts nearly perfect attendance in winter but lower attendance in summer (Metz et al. 2011). However, the applicability of this model, developed in Yellowstone National Park, Wyoming, USA, to the smaller packs and different landscape of Ellesmere is uncertain. A lower probability of attendance could partly explain the fewer muskox kills detected in summer 2017 compared to other seasons, but it could also indicate the importance of neonates and hares, which are less



detectable through hourly collar locations. Furthermore, kill rates over short periods may not accurately represent annual kill rate, as wolves generally cannot maintain high kill rates for long (Sand et al. 2008, Metz et al. 2011).

More important than kill and predation rates alone are the predator–prey ratio and the shape of the functional response, especially where many interacting factors drive population trends (Vucetich et al. 2011). This is relevant to our study, given the widespread availability of Arctic hares, the historical availability of Peary caribou, and the significant impact of weather on prey abundance and distribution. Estimating functional response curves requires data unavailable in this study.

Our research also highlighted the importance of Arctic hares to wolf diet (Tener 1952, Mech 2007). We detected hare remains at 15% of the location clusters investigated in 2018, but small prey are often under-represented by location-cluster algorithms (Palacios and Mech 2010). The population fluctuations and movements of Arctic hares are not well understood (Mech 2005, Dalerum et al. 2017, Caron-Carrier et al. 2022), although they could have additional implications for wolf predation patterns based on variation in hare availability. Our study system likely functions like wolf–ungulate–beaver (*Castor canadensis*) systems, where small prey can contribute substantially to wolf biomass intake (Benson et al. 2013, Latham et al. 2013, Gable et al. 2018).

The near disappearance of Peary caribou from Axel Heiberg Island between 2007 and the time of this study (Mallory et al. 2020) precludes any conclusions about the role of wolf predation in Peary caribou population dynamics. During this period, there were no reported weather-related die-offs, nor were there any observations of caribou moving to or inhabiting surrounding islands. Peary caribou typically occur at low densities year-round and do not engage in large-scale migrations or calving aggregations (COSEWIC 2015). Bergerud (1988) suggested that wolf densities  $>6.5$  wolves/1,000 km<sup>2</sup> could limit caribou populations. While that threshold may not apply to Peary caribou, addressing apparent competition (Holt 1977, Holt et al. 1994) has been a key issue in woodland caribou recovery efforts, especially when caribou densities are low (Seip 1992, Hayes et al. 2003, Apps and McLellan 2006, Hervieux et al. 2014, Serrouya et al. 2017). The most recent status assessment for Peary caribou (COSEWIC 2015) does not consider the near disappearance of a formerly high-density caribou population on Axel Heiberg Island (Mallory et al. 2020). A stable, high-density wolf population, primarily supported by muskoxen and hares, could influence Peary caribou, warranting further investigation in areas where the 3 species are sympatric.

## MANAGEMENT IMPLICATIONS

Muskoxen and Peary caribou are vital to the security and cultural persistence of Inuit and Inuvialuit communities. In both Nunavut and the Northwest Territories, these species are co-managed by Inuit and Inuvialuit wildlife boards, community hunter and trapper organizations, and federal and territorial governments. However, lack of knowledge about the basic ecology and current status of this animal community in the CAA complicate co-management efforts to anticipate its future dynamics in the context of rapid environmental change. We identified aspects of High Arctic wolf ecology that have implications for Peary caribou persistence or recovery: wolf populations in the High Arctic can exist on year-round territories supported by muskoxen and Arctic hares. Ungulate-biomass regressions predicted wolf density in our study area, suggesting that the models may be applicable in other areas of the High Arctic where there is concern about wolf effects on ungulates and yet no wolf monitoring. It is reasonable to expect that such wolf populations could affect Peary caribou numbers. In particular, high muskox densities supporting high wolf densities could lead to elevated predation rates on caribou, potentially depleting local herds via apparent competition. Moreover, high-density wolf populations in relatively productive areas of the High Arctic, such as our study area, could serve as important source populations for other areas of the CAA, which is an important region for the conservation of Arctic wolf–ungulate interactions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

All research activities were conducted in accordance with Government of Nunavut Wildlife Research Permits 2014–010, 2015–048, 2016–043, 2017–042, and 2018–036, and Utah State University Institutional Animal Care and Use Protocols 2365 and 2489.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available because of privacy or ethical restrictions (potential for misuse of location data to detriment of species).

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