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Weather Effects on the Haul-Out Behaviour of Ringed Seals in the Amundsen Gulf

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ABSTRACT

Ringed seals (*Pusa hispida*) use sea ice year-round in the Arctic as a platform for giving birth, raising young and moulting. Arctic ringed seal population assessments are typically conducted by aerial surveys flown in the spring, when many seals haul out. However, many factors can influence whether a seal is hauled out on the ice and available for detection. Understanding the environmental factors that impact ringed seal haul-out behaviour will reduce bias in aerial surveys. We deployed camera traps near Ulukhaktok, Northwest Territories, Canada in mid-May 2023, 2024 and 2025 facing open water leads in the sea ice to document haul-out behaviour of ringed seals under varying weather conditions. We used generalized additive mixed models to analyse the presence/absence and number of ringed seals hauled out. We found that high temperatures (> −4.3°C), low wind speeds (< 20 km/h), and high barometric pressure systems (101.4–101.8 kPa) increased the probability and number of ringed seals hauling out. We also found that haul-outs occurred at lower temperatures under conditions of low and moderate wind speeds, and that the number of seals hauled out increased at lower temperatures at low wind speeds. We identify specific 'ideal weather' parameters for aerial surveys, which will reduce availability bias when calculating density and abundance estimates.

1 | Introduction

Climate change is occurring in the Arctic at four times the rate of the global average (You et al. 2021; Rantanen et al. 2022; Dai and Jenkins 2023). The resulting decreases in sea ice cover and snowpack driven by climate warming are predicted to have significant impacts on Arctic marine mammal populations (Laidre et al. 2015; Fuirst et al. 2023). Ringed seals (*Pusa hispida*), the most abundant marine mammal species in the Arctic, rely on sea ice habitat as a platform for hauling out and pupping (Kovacs et al. 2011; Fuirst et al. 2023). Ringed seals build snow lairs to rest, hollowing out snow that accumulates over breathing holes which are actively maintained using the strong claws on their fore flippers (Smith et al. 1991; Smith and Stirling 1975). These snow lairs are also where pups are birthed and nursed in the spring, and are important for pup survival as they provide protection from predators and harsh weather conditions (Smith and Stirling 1975; Smith et al. 1991). Ringed seals are both a key component of the Arctic food web and an important traditional food (Nattiq) for communities throughout Inuit Nunangat (OHTC et al. 2016; Simon 2011). Sea ice availability directly influences ringed seal diet, which consists of ice-associated prey including Arctic cod (*Boreogadus saida*), amphipods and copepods (McLaren 1958; Lowry et al. 1980; Matley et al. 2015; Insley et al. 2021). As a result, changes in the distribution of sea ice habitat and prey could have long-term population-level impacts on ringed seals (Freitas et al. 2008; Kovacs et al. 2011; COSEWIC 2019).

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Furthering the effects of climate change, increasing industrial activity resulting from reduced sea ice cover in the Arctic is expected to have additional adverse impacts on ringed seals (Laidre et al. 2015; Hauser et al. 2018, 2026). For example, ice-breaking vessels will likely be routed through ringed seal habitat, destroying birthing lairs and haul-out platforms (Yurkowski et al. 2019) and increasing the likelihood of collisions between vessels and marine mammals (Harkonen et al. 2008; Wilson et al. 2017). Noise pollution, sourced from resource extraction and shipping, is predicted to cause behavioural disturbances in marine mammals (Halliday et al. 2017; Dingwall et al. 2024; Martin et al. 2024; Shajahan et al. 2024). Collecting population data to assess the stock of ringed seals is essential for understanding how ice-adapted marine mammals will respond to climate change and human development.

Sea ice is used as a platform for ringed seals to haul out, which occurs during the annual moult to increase skin temperature, a requirement for regeneration of the epidermis (Feltz and Fay 1966). We define a 'haul-out' as any time a seal completely exits the water onto the exposed surface of the snow and ice (i.e., not inside a lair). The peak in haul-out activity occurs between snow lair disappearance and ice break-up, typically between mid-May and mid-June (Moulton et al. 2002; Kelly et al. 2006; Lindsay et al. 2026). During this period, seals begin to spend more time out of the water and outside of snow lairs, allowing a greater proportion of seals to be available to be seen for counting during aerial surveys (Lydersen and Gjertz 1986; Kelly et al. 2006; Chambellant et al. 2012; Young et al. 2015, 2019; Von Duyke et al. 2020; Fuirst et al. 2023; London et al. 2024). This period is dependent on snow and ice conditions which have high interannual variability (COSEWIC 2019; Kelly et al. 2010).

In this study, we analyzed data from camera traps deployed on the sea ice in the eastern Amundsen Gulf, Northwest Territories (NT), Canada in mid-May 2023, 2024 and 2025. We explored how environmental factors influenced ringed seal haul-out behaviour. Previous studies have analyzed how environmental variations impact the haul-out probability of ringed and other ice-associated seals, establishing the relationship that bright, warm and calm conditions increase haul-out occurrences (Boveng et al. 2025; Carlens et al. 2006; Chambellant et al. 2012; Finley 1979; Hamilton et al. 2018; Kelly et al. 2006; Kingsley et al. 1985; Moulton et al. 2002; Smith and Hammill 1981; Stirling et al. 1982). These studies are commonly conducted using biotelemetry data to track movement in-and-out of the water (Bengtson et al. 2005; Crawford et al. 2019; Hamilton et al. 2018; Kelly and Quakenbush 1990; London et al. 2024). The use of snow lairs by ringed seals produces an added layer of complication when analyzing this data, as determining the difference between a 'dry' hauled-out seal versus a 'dry' seal in a snow lair is not possible without estimation (Lindsay et al. 2026). Camera trap studies allow for a clear determination of a hauled-out seal that would be visible during aerial surveys. Using this alternate method, we wanted to test the established patterns of environmental conditions in a study area that has not previously been analyzed for these patterns. Our study typically occurred after snow lair abandonment but before ice break-up. For our purposes, we define 'haul-out probability' as the likelihood of a haul-out occurring at a given site. This is distinct from individual haul-out probability, as individual identification was not possible from our data.

Based on the patterns observed in other regions and via telemetry or aerial survey methods, we expected that the probability of haul-outs and number of ringed seals hauled out would increase when environmental conditions are adequate for moulting: (1) Increased skin temperatures are required for epidermal regeneration (Feltz and Fay 1966), therefore warmer air temperatures would increase haul outs; (2) high pressure systems are associated with clear skies and dry weather (Spiridonov and Ćurić 2021), therefore higher barometric pressures would increase haul outs and (3) increased wind speed decreases the ability to maintain body temperature, therefore higher wind speeds would decrease haul outs.

2 | Methods

2.1 | Study Area

The study site was located in Safety Channel on the north coast of Prince Albert Sound in the eastern Amundsen Gulf, NT, Canada (Figure 1). Prince Albert Sound is 225 km long and 50 km wide where it connects to the Amundsen Gulf (Smith and Harwood 2001). Prevailing easterly winds average 18.2 km/h annually (OHTC et al. 2016). Sea ice formation usually begins in mid-October, is generally strong enough for travel by mid-November, and spring shore leads (open water cracks in the sea ice) typically appear around mid-May to mid-June (Harwood et al. 2020; OHTC et al. 2016). Sea ice breakup in the western end of Prince Albert Sound during our study years occurred on June 22nd in 2023, on June 3rd in 2024, and on June 24th in 2025 (Hall and Riggs 2021b).

Snow lair abandonment is associated with several climate proxies, including snow and air temperatures. For snow temperature, final lair abandonment is expected to occur within 4–6 days of the snow becoming isothermal, that is, when temperatures at the snow-ice interface reach 0°C (Kelly et al. 2006). We lacked in situ measurements of snow temperature, and to approximate the date of snow melt in our study area we used remotely sensed satellite data that measures temperatures at the interface between the snow or ice surface (whichever is on top) and the atmosphere (Hall and Riggs 2021a). The approximated isothermal conditions first occurred on May 4th in 2023 and on May 5th in 2024 (Hall and Riggs 2021a). In 2025, approximated isothermal conditions first occurred on May 18th which was after our study dates (Hall and Riggs 2021a). For air temperature, snow lair abandonment was estimated to occur when daily air temperatures reached an average of −2.1°C (Lindsay et al. 2026). Average air temperatures of −2.1°C were first reached on May 3rd in 2023, on May 4th in 2024, and on May 17th in 2025 (AIRS Science Team and Texeira 2013; ECCC and MSC 2023, 2024, 2025), which dates align neatly with our approximated isothermal condition dates.

2.2 | Data Collection

Each year we deployed camera traps on the sea ice to record ringed seal behaviour. Between seven and nine Reconyx HF2 Pro Covert trail cameras (Reconyx, Holmen, WI, USA) were deployed in mid-May of 2023–2025 along leads or at breathing holes in the sea ice (Table 1). Sites were chosen where ringed

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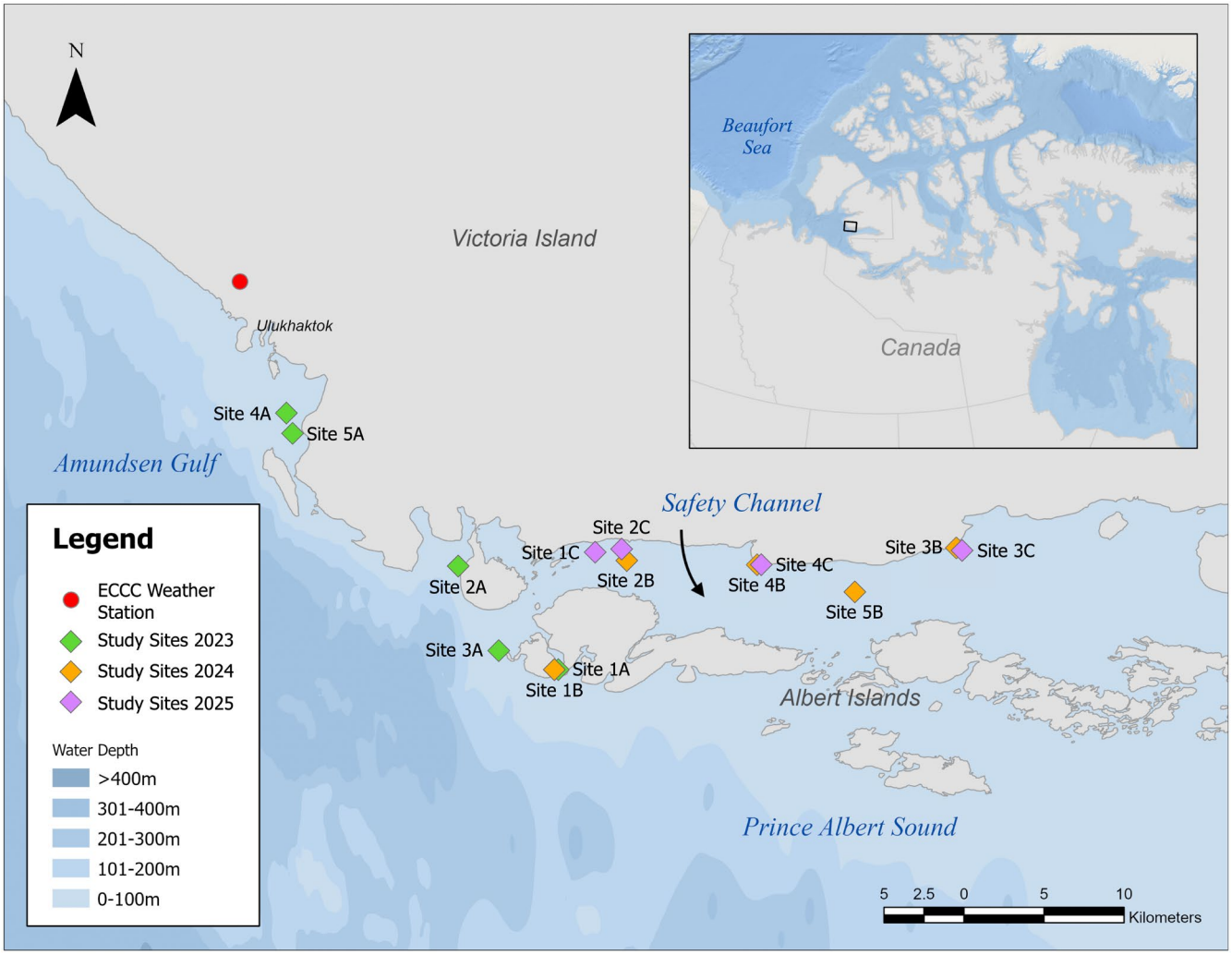

FIGURE 1 | Map of the study area in the Canadian Arctic near Ulukhaktok, NT, Canada. Diamonds indicate study sites: Green for 2023, orange for 2024, and purple for 2025. The red circle indicates the Environment and Climate Change Canada (ECCC) weather station which collects temperature (°C), wind speed (km/h) and barometric pressure (kPa) data. The ECCC Weather station is located at 70°45′46″ N, 117°48′22″ W. *Source:* Esri (2018), GEBCO (2024), NOAA, National Geographic, Garmin, TomTom, Geonames.org, Statistics Canada (2022) and other contributors.

seals were observed hauling out prior to camera installation. In 2023, we deployed two cameras facing each other and spaced 100 m apart for the first 5 days, then moved the cameras to new sites for the next 4 days (Table 1). In 2024 and 2025 at sites 1B–4B, 1C, 3C and 4C, we deployed two cameras facing each other and spaced them 100 m apart. Site 5B in 2024 and Site 2C in 2025 had only one camera and was 50 m away from a breathing hole. Cameras in 2024 and 2025 were deployed at sites between 1 and 7 days. The length of deployment in all years was dictated by concurrent work in the area, and cameras were not left out for longer periods due to uncertainty related to travelling on the sea ice at this time of year. For example, in 2024, travel to these sites was no longer possible 2 days after the cameras were removed due to sea ice melt. For all years, cameras were placed on t-posts or tripods and positioned 1.5 m above the ice surface. The motion sensors on the camera were not used to trigger image capture since a pilot study demonstrated that the motion sensor did not detect hauled-out seals. Sea ice can offer a long, unobstructed view and seals were often out of the camera's motion detection range (up to 30 m). Instead, cameras were programmed with a timelapse setup to take one image every minute and recorded the date, time, and temperature. All cameras were deployed at sites with smooth, landfast sea ice (100% ice concentration). Camera data were collected under University of Victoria Animal Use Protocols 2022-006 and 2023-013, Northwest Territories Research Licences 17180, 17491 and 17699 and Fisheries and Oceans Canada Licenses to Fish for Scientific Purposes S-23/24-3012-YK, S-24/25-3000-YK and S-25/26-4001-IN.

After camera recovery, images were uploaded to Wildtrax (https://wildtrax.ca/) for data management and processing. We manually annotated images to determine ringed seal haul-out events, as Wildtrax's automated detectors did not perform well for the sea ice environment. We defined a 'haul-out event' as an occurrence where a seal was fully out of the water and hauled out on the ice. A haul-out event began at the time in the first frame of an image where a particular seal, identified by its location within the image, was seen hauled out, and ended at the time on the last image when the seal was seen hauled out. This meant that events could begin/end with a seal entering/exiting the water or shuffling in/out of the frame of the camera yet remaining on the ice. All haul-out event durations had an error of ±59 s due to

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TABLE 1 | Summary of camera trap deployments in 2023, 2024 and 2025 near Safety Channel, NT, Canada.

Site ID	Start date	End date	No. of haul-out events	Habitat feature	Max no. seals hauled out	Max haul-out duration (h)	Mean haul-out duration (h)	No. haul outs with duration > 5 min	Mean haul-out duration > 5 min (h)
1A	2023-05-13	2023-05-17	7	Lead	4	13.0	5.4	6	6.3
2A	2023-05-13	2023-05-17	9	Lead	5	13.5	4.7	9	4.7
3A	2023-05-14	2023-05-16	17	Lead	4	8.9	2.7	10	4.2
4A	2023-05-18	2023-05-21	19	Lead	6	7.0	2.7	16	3.2
5A	2023-05-18	2023-05-21	10	Lead	3	8.0	2.1	8	2.6
1B	2024-05-12	2024-05-19	108	Lead	10	13.5	1.3	43	3.2
2B	2024-05-13	2024-05-19	4	Lead	1	0.0	0.0	—	—
3B	2024-05-13	2024-05-19	10	Lead	2	14.5	4.2	5	8.3
4B	2024-05-15	2024-05-16	1	Lead	1	2.6	2.6	1	2.6
5B	2024-05-15	2024-05-19	2	Breathing hole	1	37.9	29.2	2	29.2
1C	2025-05-12	2025-05-17	9	Lead	6	8.0	5.1	8	5.8
2C	2025-05-14	2025-05-17	1	Breathing hole	1	9.5	9.5	1	9.5
3C	2025-05-12	2025-05-17	50	Lead	8	14.0	3.5	32	5.5
4C	2025-05-11	2025-05-17	63	Lead	9	32.4	5.3	42	7.9

Note: A haul-out event is defined as when a seal is fully out of the water and hauled out on the ice. Duplicate haul-out events captured by both cameras at a single site were removed during data processing to avoid double counting of seals. Max number of seals hauled out indicates the total number of seals hauled out in a single image and does not indicate group size.

the image capture settings. Ringed seals seen swimming in the water along the crack were tagged as 'travelling' but were not considered a haul-out event. At sites where two cameras were deployed, seals seen beyond the opposing camera (100 m apart), were included as haul-out events.

We did not assign groups; rather, each individual seal per image was a haul-out event (Figure 2). Where there were multiple seals hauled out close to one another, it could be difficult to determine when an event ended and began. This error could underestimate the number of seals hauled out but would not impact the presence/absence data. Image sets from sites with multiple cameras were analyzed concurrently to avoid double counting the same haul-out event. We could not determine sex or age from camera images, nor could we identify individuals.

Loss of visibility due to heavy fog, snow, displacement of the camera, or other weather events significantly reduced the field of view (FOV). The images captured during reduced FOV were considered out of range, so these data were removed from analysis as it was impossible to determine if a seal was present.

2.3 | Weather Data

We collected weather data from an Environment and Climate Change Canada (ECCC) weather station at Ulukhaktok airport (ECCC and MSC 2023, 2024, 2025), located 30 km on average from our study sites (range: 8–48 km; elevation: 36 m; Figure 1). From the station, we extracted hourly wind speed (km/h), barometric pressure (kPa) and temperature (°C). We did not use the temperature data collected by the camera traps (Figure 2) because direct sun exposure caused large temperature spikes, and we did not have local temperatures for validation/calibration (Figure S1). For visualization during our analysis, we divided wind speed data into terciles and determined the mean of each tercile (low = 10.5 km/h, medium = 18 km/h and high = 30 km/h) using the interactions package (Long 2019) in R (R Core Team 2024).

2.4 | Statistical Modelling

Overall, we modeled the probability of haul-outs and number of seals hauled out. We conducted all of our analyses in R (R Core Team 2024). We merged the image data into site-level timelines, with an output of the presence-absence (1,0) of seals and the total number of seals present at each site per minute. Data were then aggregated by site and hour, where we used the mean value of the presence-absence data to determine the proportion of each hour at each site where there was at least one seal hauled out. The number of seals data was also aggregated by site and hour, where we used the maximum number of seals hauled out per hour at each site. This aggregation was done to match the resolution of the weather station data, avoid pseudoreplication, and

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FIGURE 2 | Camera trap image taken at site 1B facing a lead in the sea ice. Each seal hauled out constitutes one haul-out event, so the eight ringed seals captured in this image represent eight separate haul-out events. Date, time and ambient temperature can be seen at the top of the image.

minimize temporal autocorrelation. We then used generalized additive mixed models to model haul-out behaviours.

Using two response variables, the presence of hauled-out seals and the number of seals hauled out per hour, we designed two sets of candidate models with identical fixed and random effects (Tables 2 and 3). To model the presence-absence of seals, we used a binomial distribution (Hahn and Ohyama 2023) with a clog-log link because there were significantly more zeros than ones in our data (Zuur et al. 2009). To model the number of seals hauled out, we used a negative binomial distribution due to the overdispersion of our data (overdispersion test: $p < 0.001$) using the performance package (Lüdecke et al. 2021). We used site ID as a random intercept to account for site-level variations. To account for temporal autocorrelation, we included hour-of-day as a cyclic cubic regression spline, and the interaction between hour-of-day and day-of year as a tensor product interaction using a cyclic cubic regression spline (knots (k) = 24) and a thin-plate regression spline ($k = 10$) (Mitchell et al. 2020; London et al. 2024). In both sets of models, we tested haul-outs (presence/absence and number) as functions of varying combinations of temperature, barometric pressure, wind speed, and interactions between the variables using thin-plate regression splines (Tables 2 and 3). The interaction between wind speed and temperature was included as a tensor product interaction. For smoothers, we used $k = 5$ for the barometric pressure curves (Keele 2008), and the default k value ($k = 10$) for the temperature and wind speed curves (Tables S1 and S2). We also ran intercept-only and univariate models as comparisons to the more complex models (Tables 2 and 3). Models were run using the mgcv package (Wood 2011, 2017) following a generalized additive model (gam()) framework.

For each set of candidate models, we used Akaike's information criterion (AIC) to assess how well a model fit the observed data relative to other candidate models (Akaike 1973). We calculated the difference in AIC values (ΔAIC) and model weights (Tables 2 and 3) using the bbmle package (Bolker and R Development Core Team 2023). ΔAIC is the difference in AIC between a model and the minimum AIC model (Akaike 1978, 1979; Wagenmakers and Farrell 2004). Model weights provide a normalized likelihood for each model and show the favourability of one candidate model over another (Burnham and Anderson 2001; Wagenmakers and Farrell 2004). To evaluate model fit, we calculated receiver

TABLE 2 | Summary of candidate models predicting the probability of ringed seal haul-out occurrences.

Fixed effects	AIC	ΔAIC	Weight
s(temperature) + s(wind speed) + s(barometric pressure, $k = 5$) + ti(temperature, wind speed)	1086.5	0.0	1
s(temperature) + s(barometric pressure, $k = 5$)	1177.9	91.4	< 0.001
s(temperature) + s(wind speed) + ti(temperature, wind speed)	1191.1	104.6	< 0.001
s(barometric pressure, $k = 5$)	1567.6	481.1	< 0.001
s(wind speed)	1572.2	485.7	< 0.001
s(temperature)	1644.2	557.6	< 0.001
Null	1674.3	587.7	< 0.001

Note: We included site ID as a random intercept and used hour-of-day and day-of-year to account for temporal autocorrelation in all models. $\Delta_i AIC = [AIC_i - \min(AIC)]$, the difference between the model AIC and the minimum AIC of the candidate models.

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operating characteristics (ROC) and area under the ROC curves (AUC), which provides an assessment of sensitivity to false positives and measures the model performance (Shabani et al. 2018). AUC values above 0.7 indicate confidence in the predicted probabilities when compared to the observed data (Brotons et al. 2004; Shabani et al. 2018).

Last, we evaluated models for zero-inflation and temporal autocorrelation using test functions from the DHARMa package (Hartig 2016). Zero-inflation occurs when there are more zeros than expected in the data (Zuur et al. 2009). We tested this by simulating a new dataset from our fitted models and comparing the number of observed zeros to the number of simulated zeros, where a ratio approaching one indicates a match between the observed and simulated zeros and therefore no zero-inflation (Hartig 2016). We tested for temporal autocorrelation by performing a Durbin-Watson (DW) test on uniformly scaled residuals and plotting them against time to assess first-order autocorrelation (Durbin and Watson 1950; Hartig 2016). The resulting statistic (DW) can range from 0 to 4 where a DW ≈ 2 indicates that there is no first-order autocorrelation (Krämer 2025).

TABLE 3 | Summary of models estimating the number of hauled-out ringed seals.

Fixed effects	AIC	ΔAIC	Weight
s(temperature) + s(barometric pressure, $k = 5$) + s(wind speed) + ti(temperature, wind speed)	2574.8	0.0	1
s(temperature) + s(wind speed) + ti(temperature, wind speed)	2655.2	80.4	< 0.001
s(temperature) + s(barometric pressure, $k = 5$)	2682.0	107.2	< 0.001
s(wind speed)	3130.6	555.9	< 0.001
s(barometric pressure, $k = 5$)	3138.5	563.7	< 0.001
s(temperature)	3197.2	622.4	< 0.001
Null	3275.5	700.7	< 0.001

Note: We included site ID as a random intercept and hour-of-day and day-of-year to account for temporal autocorrelation in all models. We used a negative binomial distribution. $\Delta_i AIC = [AIC_i - \min(AIC)]$, the difference between the model AIC and the minimum AIC of the candidate models.

3 | Results

We deployed between seven and nine camera traps each year; for 9 days (May 13–21) in 2023, 8 days (May 12–19) in 2024 and 7 days (May 11–17) in 2025, resulting in a cumulative total of 2619 h of data and 157,090 images. We collected data from five sites in 2023, five sites in 2024, and four sites in 2025 (Figure 1). Cameras at site 4B (Figure 1) had a later start date and a shorter duration compared to the other 2024 deployments because a polar bear killed a hauled-out ringed seal and knocked over both cameras the day after deployment (Figure 3). Cameras at site 3A (Figure 1) had a shorter deployment duration compared to the other 2023 deployments because both cameras fell over due to melting ice.

Weather during our study dates was variable (Figure S2); 2023 had higher mean barometric pressure conditions (2023 mean = 101.6 kPa; 2024 mean = 101.1 kPa; 2025 mean = 101.4 kPa), 2024 had the highest mean wind speeds (2023

FIGURE 3 | Camera trap image taken at site 4B facing a lead in the sea ice. Here, a ringed seal was killed by a polar bear, which proceeded to knock over the deployed cameras. The second camera trap at this site can be seen in the background.

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mean = 17 km/h; 2024 mean = 25 km/h; 2025 mean = 14 km/h), and 2025 was colder than the two previous years (2023 mean = −2.4°C; 2024 mean = −1.6°C; 2025 mean = −8.7°C). Comparison of the weather conditions during the potential haul-out peak dates (snow lair abandonment to sea ice breakup: May 9–June 21, 2023; May 10–June 2, 2024; May 23–June 23, 2025) showed that the conditions present during our study dates were relevant to the general weather observed during the peak timing (Figure S3).

From the image data, we recorded 62, 125 and 123 haul-out events in 2023, 2024 and 2025, respectively for a total of 310 haul-out events (Table 1). Compared to the 2023 data, haul-out events recorded in 2024 and 2025 had an uneven distribution across sites; site 1B (Figure 1) had 108 haul-out events, with only 17 haul-out events occurring at all other sites in 2024, and 92% of haul-out events occurred at sites 3C and 4C in 2025 (Table 1). The maximum number of ringed seals hauled out in a single image was 10 (Table 1).

Haul-out event duration was variable: minimum duration was 1 min while the maximum duration was 37.9 h (Table 1). In 2023 and 2025, the average haul-out event durations (2023 = 3.2 ± 3.1 h; 2025 = 4.6 ± 5.1 h) were much higher compared to 2024 (1.9 ± 4.6 h). However, only 41% of haul-out events recorded in 2024 had a duration longer than 5 min (Table 1).

3.1 | Probability of Seal Haul-Out

Based on AIC values, the best supported model predicting the probability of seals hauling out included the fixed effects of temperature, wind speed, barometric pressure, and the interaction between temperature and wind speed (Table 2). From this model, we found increasing temperature (Figure 4a), increasing barometric pressure (Figure 4c), and decreasing wind speeds (Figure 4b) were associated with an increase in haul-out probability. At temperatures above −4.3°C and wind speeds below 20 km/h, there was a greater than 50% probability of a seal haul-out occurring. At low and medium wind speeds, haul-out probabilities increased at cooler temperatures (−8.1°C to −4.3°C; Figure 4d) whereas haul-out probability increased at high wind speeds when temperatures exceeded −1.5°C (Figure 4d). AUC value was 0.84, indicating good model fit. Zero inflation (ratio

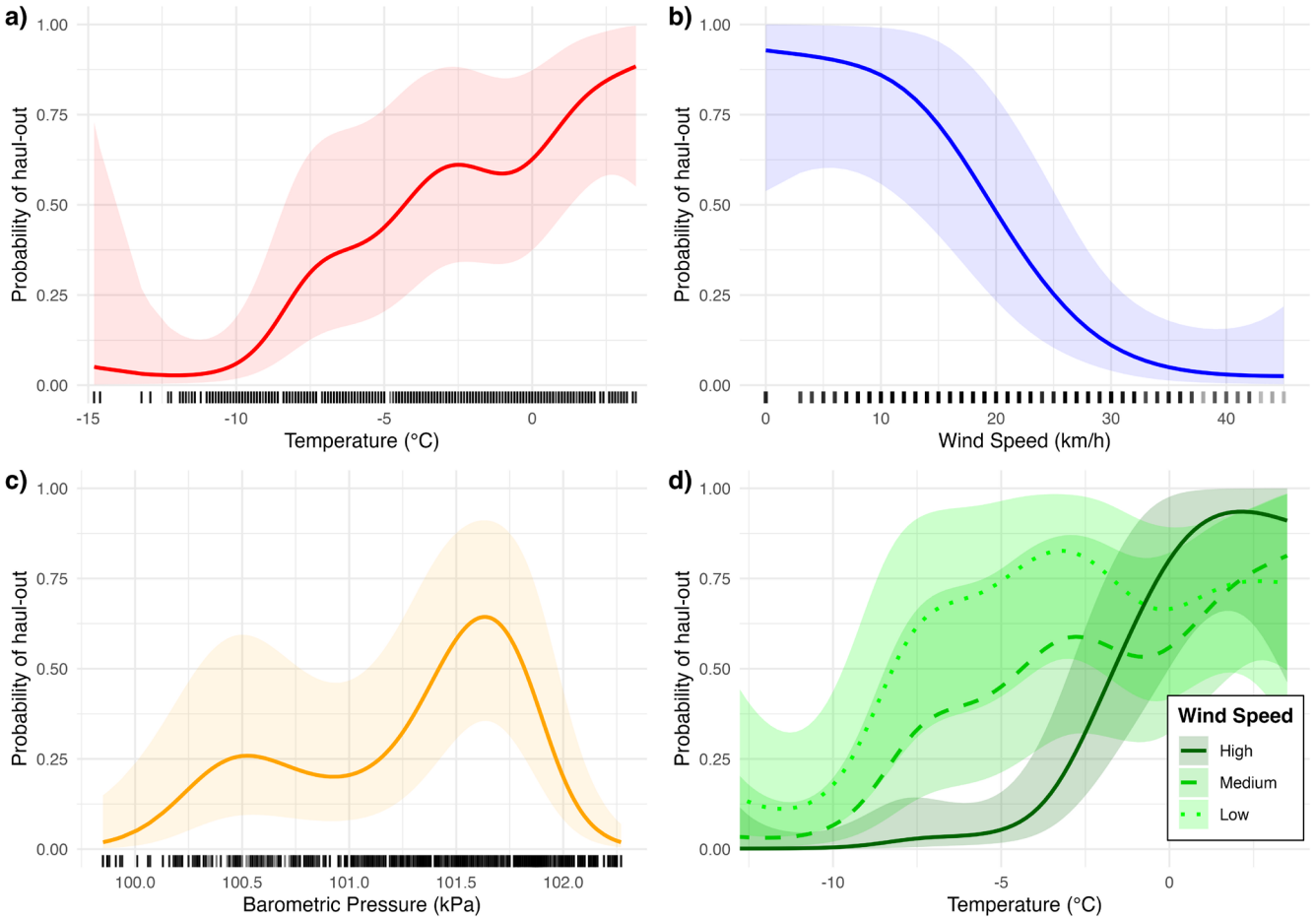

FIGURE 4 | Influence of weather covariates (a) temperature (°C), (b) wind speed (km/h), and (c) barometric pressure (kPa) on the probability of ringed seal haul-outs, with shaded ribbons showing 95% confidence intervals. (d) The interaction of temperature and wind speed, with wind speed data divided into terciles and modelled the mean of each tercile (low = 10 km/h, medium = 18 km/h, high = 30 km/h). Data were collected in 2023, 2024 and 2025 from Safety Channel, NT, Canada. Black tick marks along the *x*-axis indicate the distribution of our raw data used in the models. Wind speed was recorded to the nearest whole number, whereas temperature and barometric pressure were recorded to one and two decimal places, respectively. Predictions in panels a–c were generated by holding the non-focal covariates at their mean values.

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of observed to simulated zeros = 0.96) and temporal autocorrelation tests (DW = 2.2) showed no cause for concern.

3.2 | Number of Seals Hauled Out

The top model for the number of seals hauled out included the fixed effects of temperature, wind speed, barometric pressure, and the interaction between temperature and wind speed (Table 3). For the temperature and wind speed interaction, low wind speeds showed increasing numbers of seals hauling out at lower temperatures (−9.1°C) compared to medium and high wind speeds, which showed an increase in haul-out numbers occurring only at warmer temperatures (med = −7.3°C; high = −0.8°C; Figure 5d). Overall, higher numbers of seals hauled out at lower wind speeds regardless of temperature (Figure 5d). The number of hauled-out seals showed a similar temperature threshold as the probability models: the number of seals hauled out showed a positive relationship with temperatures above −5.8°C and wind speeds below 21 km/h (Figures 5a and 5b). AUC value was 0.91, indicating good model fit. Zero inflation (ratio of observed to simulated zeros = 1.0) and temporal autocorrelation tests (DW = 1.9) showed no cause for concern.

4 | Discussion

We analyzed weather and camera trap data collected in the Western Canadian Arctic to understand environmental influences on ringed seal haul-out behaviour. Using generalized additive mixed models, we modeled ringed seal haul outs and found that at higher temperatures (> −4.3°C), low wind speeds (< 20 km/h), and high barometric pressure (101.4–101.8 kPa), ringed seals are more likely to haul out (Figures 4 and 5). We also found that ringed seals haul out in warm temperatures, regardless of wind speeds. These results provide data-driven weather-based correction factors for aerial survey population estimates.

Seal haul-out behaviour can influence the quality of data collected during aerial surveys and is known to be influenced by weather conditions (Reeves 1998; Kelly et al. 2006; Frost et al. 2004; Moulton et al. 2002). Aerial surveys are the primary method used to conduct population and density estimates of ringed seals (Kelly et al. 2006;

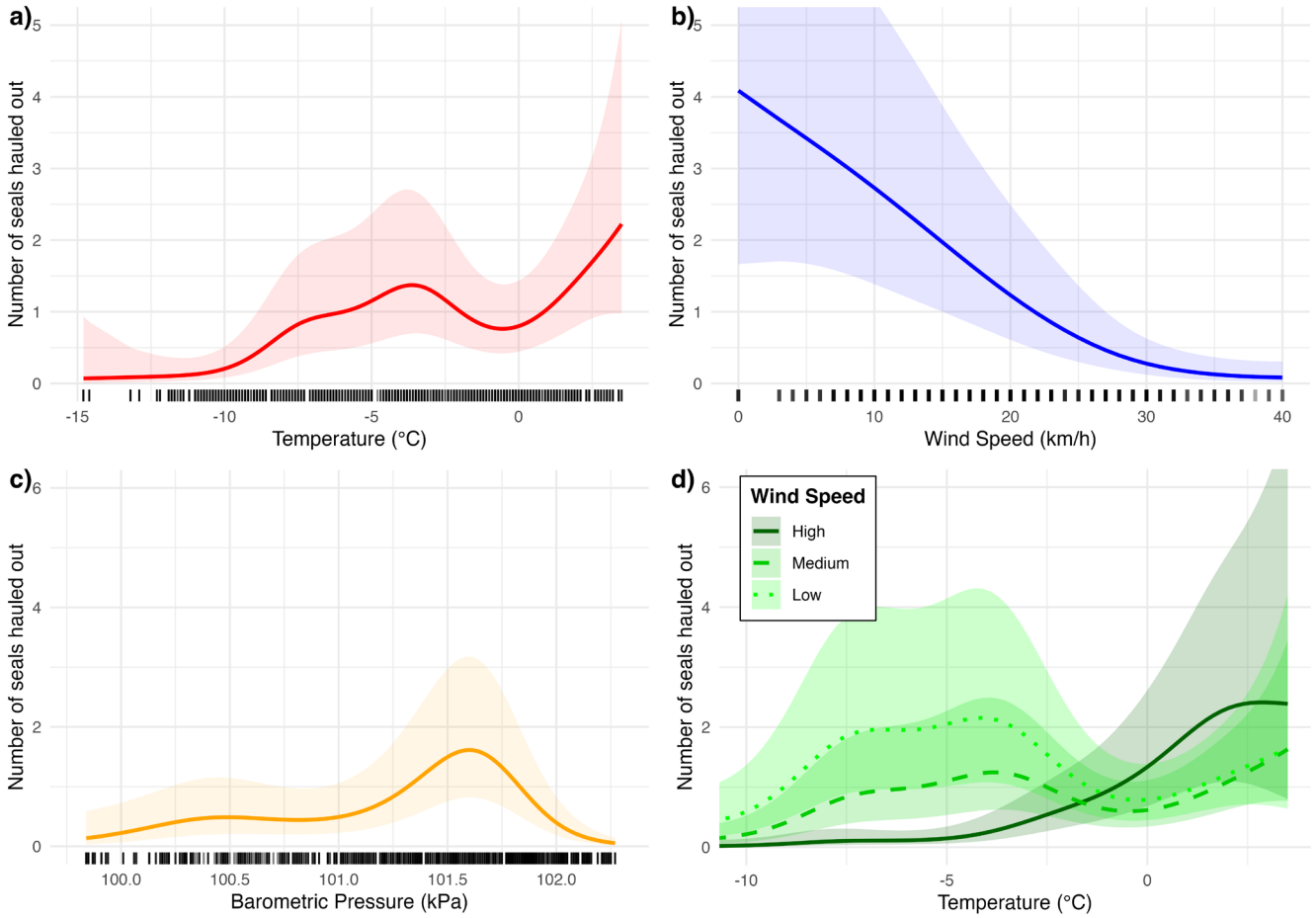

FIGURE 5 | Influence of weather covariates (a) temperature (°C), (b) wind speed (km/h) and (c) barometric pressure (kPa) on the number of ringed seals hauled out, with shaded ribbons showing 95% confidence intervals. (d) The interaction of temperature and wind speed, with wind speed data divided into terciles and modelled the mean of each tercile (low = 10 km/h, medium = 18 km/h, high = 30 km/h). Data were collected in 2023, 2024 and 2025 from Safety Channel, NT, Canada. Black tick marks along the *x*-axis indicate the distribution of our raw data used in the models. Wind speed was recorded to the nearest whole number, whereas temperature and barometric pressure were recorded to one and two decimal places, respectively. Predictions in panels a-c were generated by holding the non-focal covariates at their mean values.

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Chambellant et al. 2012; Young et al. 2015, 2019), so understanding how weather conditions impact haul-out behaviour may reduce bias present in aerial surveys as the seals can only be counted when they are hauled out (Conn et al. 2012; Boveng et al. 2025). In our models, haul-out probability was greater than 50% for temperatures above −4.3°C and wind speeds below 20 km/h (Figure 4). Models estimating the number of hauled-out seals also showed similar thresholds, with the number of haul outs increasing for temperatures above −5.8°C, and wind speeds below 21 km/h (Figure 5). Many other analyses have recognized the trend that warmer temperatures, clear skies, and lower wind speeds increased ringed seal haul outs, but the thresholds for survey conditions are rarely quantified (Boveng et al. 2025; Carlens et al. 2006; Chambellant et al. 2012; Finley 1979; Hamilton et al. 2018; Kelly et al. 2006; Kingsley et al. 1985; Moulton et al. 2002; Smith and Hammill 1981; Stirling et al. 1982). For example, Kelly et al. (2006) reported an increase in haul-outs when temperatures were between −10°C and 8°C, while wind speeds above ≈20 km/h saw significant decreases in haul-outs when studying ringed seals in the near-shore Alaskan Beaufort Sea. Our models show that ideal conditions for conducting ringed seal aerial surveys are low winds (0–20 km/h), warm temperatures (above −4.3°C), and no cloud cover (high barometric pressure; 101.4–101.8 kPa). Surveys in sub-optimal conditions may result in population underestimation (e.g., few seals are hauled out), or population bias (e.g., perhaps only dominant males are hauled out in high winds, as seen in other pinniped species; Breed et al. 2006; Jones et al. 2021). Survey periods may not always be flexible to align with ideal weather conditions, since the logistics required for conducting an Arctic survey are complex. However, our results provide guidelines for using correction factors based on temperature and wind speed thresholds, for example, when calculating population estimates based on aerial survey data.

Peak haul-out behaviour for ringed seals is variable year-to-year, as it is highly dependent on the timing of snow and ice melt (COSEWIC 2019; Kelly et al. 2010). Our study dates occurred in mid-May, beginning shortly after snow lair abandonment brought on by increasing air and snow temperatures in 2023 and 2024 (AIRS Science Team and Texeira 2013; Hall and Riggs 2021a; Kelly et al. 2006; Lindsay et al. 2026). The end of the peak haul-out period is influenced by ice break-up dates, which showed high interannual variation between our study years (Kelly et al. 2006; Hall and Riggs 2021a). Our sampling dates in 2025 took place before the defined 'peak haul-out' window, with temperatures during the study reaching a maximum of −3.9°C (ECCC and MSC 2025). Even with these 'poor' conditions we recorded 123 haul-out events, a result that is 2× the number of seals observed during our 'milder' 2023 study period. As temperatures increase in the Arctic, it is reasonable to expect that the timing of ringed seal haul-outs will change. For example, Finley (1979) reported that during their 1977 study period, cooler temperatures allowed deep snow to remain present on the ice until early June. This deeper snow allowed for later snow-lair abandonment, which can then explain their observations that ringed seal haul-outs in the nearby Barrow Strait area did not peak until mid-June (Finley 1979). Moreover, significant warming has occurred in the Arctic since 1977 and conditions that were previously seen in mid-June are likely happening significantly earlier now such as in mid-May. Harwood et al. (2020) noted that stable landfast ice in the western Prince Albert Sound is clearing ≈4 days earlier per decade. Aerial survey timing should therefore be dictated by snow and ice conditions as impacted by weather and will likely need to adapt over time based on the changing environment.

While our results have practical applications to survey methods, the ecophysiology aspects of seal haul-out behaviour are largely unexplored. Haul-out behaviour is thought to increase skin temperature, as the metabolic cost of moulting is high (Feltz and Fay 1966; Thometz et al. 2021). The overall moulting period for ringed seals typically lasts for ≈1 month between May and June, during which time they modify their behaviour by spending less time foraging and more time on the ice to facilitate tissue regeneration (Thometz et al. 2021; Von Duyke et al. 2020). However, wind exerts a cooling effect on the body, increasing the metabolic requirements to maintain body temperature (Blix 2016). We found that wind speed showed a negative relationship with haul-out behaviours (Figures 4 and 5), particularly when modelled with the interaction between wind speed and temperature. This result indicates that at lower wind speeds, lower ambient temperatures may be adequate to increase skin temperatures (Figures 4 and 5). In contrast, at higher wind speeds, warmer temperatures may be required to combat the cooling effect driven by these stronger winds (Figures 4 and 5). Decreasing sea ice extent in the Arctic during the summer months may have considerable impacts on the energetic burden of moulting. Without sea ice available as a haul-out platform there could be negative consequences for ringed seal populations, including declining body conditions as adequate haul-out platforms shift further from productive foraging habitat or onto terrestrial platforms (Kovacs et al. 2011; Von Duyke et al. 2020; Thometz et al. 2021; Niemi et al. 2023). Future studies should focus on understanding the specific temperatures required for ringed seal skin cells to undergo epidermal regeneration and the amount of time required to maintain these temperatures to moult.

In addition to having thermoregulatory effects, wind may also influence haul-out behaviour because of altered predation risk. From a seal's perspective, high wind speeds may diminish their ability to detect predators, such as polar bears, via olfaction (smell) and audition (hearing), thus potentially increasing their risk of predation. Olfactory sensitivity in phocids has not been studied extensively, though it is known to be important when seals are out of the water based on observations of foraging behaviour (Hanke and Reichmuth 2022; Kim et al. 2013; Kowalewsky et al. 2005) and the production of chemical cues (Hanke and Reichmuth 2022; Hardy et al. 1991; Ryg et al. 1992). Audition is known to impact predator detection in seals (Deecke et al. 2002; Hanke and Reichmuth 2022). Though hearing sensitivity out of the water is lower than in-water, ringed seal escape responses are triggered by auditory disturbances (Born et al. 1999). Strong winds may mask the sound of predators and therefore increase seal predation risk (Cherry and Barton 2017). Generally, decreased wind speeds are expected to allow better predator detection in other Arctic pinniped species (London et al. 2024). Second, if seals perceive risks associated with predation, grouped haul-outs during the moulting period may be an anti-predator behaviour; large group size could protect individuals through dilution of risk (Vine 1973; Creel et al. 2014), and may allow for better predator detection (da Silva and Terhune 1988). It follows then that larger group sizes would be hauled out during optimal polar bear hunting conditions (i.e., wind speeds <21.6 km/h; Figure 5b; Togunov et al. 2017). Understanding how haul-out probabilities are impacted by the presence of another hauled-out seal requires further study.

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Although our study offers insights into seal behaviour, there are a number of limitations. First, understanding how cloud cover influences haul-out behaviours at fine spatial resolution is important; fewer clouds present would increase solar radiation, allowing for greater warming of epidermal cells than ambient temperature alone (Feltz and Fay 1966; London et al. 2024). However, we lacked cloud cover data at fine spatio-temporal resolutions as this was not a variable collected by the ECCC weather station during our study dates. We recommend further analysis using cloud cover data with a higher spatial and temporal resolution, which would increase the precision of a correction factor. Additionally, the weather conditions observed at the ECCC weather station may not precisely match the weather conditions at each of our camera sites, adding more uncertainty that could be corrected using weather data with a higher temporal and spatial resolution. However, it is worth noting that government-run meteorological authorities provide environmental data that is highly available and is what surveyors are most likely to use when determining survey timing.

Evaluating camera trap data allows for more specific behavioural analysis, including group haul-outs, vigilance, and anti-predator strategies (da Silva and Terhune 1988; Carlens et al. 2006; Survilienė et al. 2016; London et al. 2024; Niemi et al. 2023). Additionally, data from camera traps allows for more individuals to be monitored and provides broader representation of population-level behaviour compared to tagging individuals with bio-loggers, which would only represent a smaller subset of the population (London et al. 2024; Niemi et al. 2023). Analysis of Arctic seal haul-out behaviour using wet/dry sensors on satellite bio-loggers has been conducted previously (Hamilton et al. 2014; Ver Hoef et al. 2014; Olnes et al. 2020; London et al. 2024; Crawford et al. 2019), however, wet/dry sensors introduce analytical challenges for long-term analysis of ringed seals because of their use of snow lairs (Lindsay et al. 2026); the sensors cannot differentiate between a 'dry' ringed seal that is hauled out versus a 'dry' ringed seal that is in a snow lair (unavailable for aerial detection). Combining the bio-logger and camera trap data collection methods, as done by Niemi et al. (2023) when studying the Saimaa ringed seal, could allow for a wider-reaching analysis of haul-out behaviour and reduce some of the biases introduced by either method individually.

We recommend our work to improve estimates for when aerial surveys should be conducted to collect population data of this species, correct for seals not hauled out, and aid in interpretation of past survey results. Continuous monitoring of ringed seals and the impacts of decreasing ice cover and increasing temperatures caused by climate change are important, as seals play a key role in the Arctic ecosystem as both predator and prey and are also an important subsistence species for Inuit. Better understandings of group haul-out behaviours and the ecophysiology of moulting requirements would fill a knowledge gap and help interpret survey results.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Comparison of temperature (°C) recorded by the deployed camera traps (red) and by the ECCC weather station (blue) during our 2023, 2024, and 2025 study period. Days with increased sun exposure experienced significant spikes in the camera temperature. Camera trap data are shown for each site, taken as an average of the camera temperature recorded at sites with multiple cameras. **Table S1:** Comparison of AIC values for probability of haul-out model with k values specified. **Table S2:** Comparison of AIC values for number of seals hauled-out model with k values specified. **Figure S2:** Comparison of the temperature (°C), wind speed (km/h), and barometric pressure (kPa) during our 2023 (green), 2024 (orange), and 2025 (purple) study dates. **Figure S3:** Comparison of the weather conditions present during the potential peak haul-out period for ringed seals (May 9th–June 21st 2023; May 10th–June 2nd 2024; May 23rd–June 23rd 2025) and during our study periods (May 13th–21st 2023; May 12th–19th 2024; May 11th–17th 2025).

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