Dynamic Lake Ice Conditions Shape Caribou Water-Crossing Behavior in the Arctic

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Abstract

Successful animal migration hinges on navigation and decision-making in dynamic environments. Yet, how individuals navigate transient, fine-scale landscape barriers, such as seasonally ice-covered water bodies, remains poorly understood. Understanding these responses is critical for forecasting migration routes and connectivity under global change. In the Arctic, rising temperatures are causing earlier ice melt and later freeze-up, reshaping landscape permeability and potentially disrupting migration routes for overland migrants, such as barren-ground caribou *(Rangifer tarandus)*, a keystone Arctic species, which relies on frozen lakes and rivers for efficient spring travel to calving grounds. While caribou generally prefer ice to open water, behavioral responses to changing ice conditions have not been quantitatively assessed. We analyzed 20 years (2001-2021) of GPS data for 406 adult caribou and daily MODIS land surface albedo to examine lake-crossing decisions at Contwoyto Lake, a long (>100 km) glacial lake in northern Canada. We classified transit events as crossing or circumnavigation based on GPS trajectories relative to lake boundaries and linked behavioral decisions to spatially and temporally resolved ice conditions. Our models revealed distinct seasonal drivers. Spring crossing decisions were shaped by intermediate-scale ice conditions, with a behavioral threshold at a path-averaged annual albedo percentile rank of 0.56, corresponding to intermediate late-spring melt conditions when lake ice transitions from continuous cover toward fragmented surfaces. In fall, when the lake was ice-free, movement-related factors such as relative speeds along alternative routes better explained behavior. Our findings show how ice acts as a seasonal behavior filter, shaping functional connectivity through perceptual and energetic constraints. Although developed for caribou, this framework is transferable across species and systems. By linking high-resolution, spatiotemporal remote sensing to individual behavior, our framework detects fine-scale behavioral

45 thresholds in response to dynamic, climate-sensitive landscape features, supporting predictive

46 monitoring of climate-driven shifts in migratory behavior and constraints on adaptive limits.

1. Introduction

Seasonal long-distance migration is a fundamental ecological strategy that enables animals

to track dynamic resources, avoid predators, and access critical reproductive habitats (Fryxell and

Sinclair 1988b; Avgar et al. 2014). This strategy allows larger populations to live and reproduce

in regions that are only seasonally suitable (Fryxell and Sinclair 1988a; 1988b; Fryxell et al. 1988).

However, climate change and anthropogenic development are altering the spatial and temporal

distribution of resources, challenging the persistence of migratory species that depend on

predictable large-scale movements (Wilcove and Wikelski 2008; Harris et al. 2009; Chen et al.

2011; Middleton et al. 2013; Xu et al. 2021; Kauffman et al. 2021; Sutherland 1998).

While some adaptations of migratory species to changing environmental conditions may

be genetically based (Alerstam et al. 2003; Anderson et al. 2013), long-lived social migrants often

rely more heavily on a combination of social interactions —from older members to newer ones—

and shared memories to navigate new settings (Mueller et al. 2013; Teitelbaum et al. 2016; Berdahl

et al. 2018; Jesmer et al. 2018; Gurarie et al. 2021; Aikens et al. 2022). For example, recent work

documented a 500-km winter range shift in the Western Arctic caribou herd, apparently shaped by

the collective memory of poor conditions in previously favored areas (Gurarie et al. 2024). While

this behavioral flexibility reflects the potential for adaptive reconfiguration of movement, it also

reveals imperfect outcomes, highlighting how even socially transmitted strategies may struggle to

keep pace with rapid environmental change. Despite these insights, key knowledge gaps remain.

The mechanisms by which environmental cues influence migratory behavior are still poorly

understood, particularly at the fine spatiotemporal scales at which animals make movement

decisions affected by global changes. Although numerous studies have examined species

distribution shifts (Parmesan 2006) or population-level consequences of global warming

(Mysterud et al. 2001; Coulson et al. 2001; Post and Forchhammer 2008), few studies have linked

fine-scale individual behavioral decisions during migration to real-time environmental conditions

across dynamic landscapes under large-scale climate change (Stien et al. 2010; Barrett et al. 2012).

This lack of mechanistic understanding hinders our ability to anticipate how migratory species will

respond to future climate scenarios.

In cold regions, seasonal ice serves as a key environmental feature that modulates animal

movement. Acting as a temporary bridge across aquatic barriers, ice forms vital migration

corridors for terrestrial species (Banfield 1954b). However, with Arctic warming proceeding

nearly four times faster than the global average (Screen and Simmonds 2010; Jeong et al. 2014;

Rantanen et al. 2022), the timing and reliability of ice formation have become increasingly erratic.

Long-term observational records across the Northern Hemisphere reveal earlier break-up and later

freeze-up of lakes and rivers (Magnuson et al. 2000), shortening the seasonal window for ice-

supported movement. These shifting ice regimes threaten the functional connectivity of aquatic-

terrestrial landscapes (Leblond et al. 2016), increasing detour costs, delaying access to calving

grounds, and elevating mortality risks during crossings (Miller and Gunn 1986).

Caribou and reindeer (both *Rangifer tarandus*), widespread circumpolar ungulates (*family

Cervidae*) in Arctic areas (Feldhamer et al. 2003; Hummel and Ray 2008), exemplify the

challenges posed by changing ice conditions. These migratory ungulates undertake long-distance

terrestrial migrations of up to 1000 km annually between calving and wintering grounds (Fancy et

al. 1989; Berger 2004; Joly et al. 2019), often relying on ice-covered water bodies as critical

overland migration pathways. Some populations, such as the Peary caribou (Jenkins et al. 2016;

Gautier et al. 2022) and the Dolphin and Union caribou (Poole et al. 2010), even migrate across

sea ice between islands, underscoring the ecological importance of ice as connective corridors.

Although caribou are capable swimmers, open water, particularly during ice breakup,

presents a more hazardous and energetically costly environment for movement. For example,

caribou that break through poor-quality ice may suffer severe hemorrhage or trauma when

attempting to escape or even succumb to shock and exposure (Miller and Gunn 1986). Even after

escaping, weakened individuals are more vulnerable to predation (Banfield 1954a). In contrast,

stable ice surfaces provide flat, vegetation-free travel routes that facilitate rapid movement and

predator detection (Mysterud and Østbye 1999). As ice loss accelerates, open water bodies

increasingly act as dispersal barriers, forcing caribou to either make long detours (Leblond et al.

2016) or swim, which is less efficient and increases the risk of exhaustion (Fish 1994). Energy loss

and delays are especially consequential during spring migration, when delayed arrivals may disrupt

highly synchronized birthing periods, reducing calf survival and affecting population dynamics

(Gurarie et al. 2019; Couriot et al. 2023). In contrast, fall movements tend to be more nomadic and

flexible. The dramatic population decline of the Bathurst herd, from approximately 480,000

individuals to fewer than 7,000 over the past three decades (Adamczewski et al. 2022), alongside

broader global declines in ungulate migrations (Harris et al. 2009; Tucker et al. 2018), underscores

the urgency of understanding how shifting ice phenology affects migratory behavior in the Arctic.

Despite growing interest in Arctic lake ice trends (Livingstone 2000; Benson et al. 2012;

Sharma and Magnuson 2014), most phenological studies rely on long-term in-situ records from

large, well-monitored lakes. These observations typically lack consistent definitions for freeze-up

and break-up dates (Eklund 1999; Magnuson et al. 2000; see Appendix S1), overlook within-lake

spatial variation, limiting their relevance for understanding localized environmental cues. Yet such

fine-scale variation may be critical for migratory animals making real-time movement decisions.

To address these challenges, a variety of remote sensing approaches have been employed to

monitor ice dynamics in lakes and rivers (see Appendix S1). Moderate Resolution Imaging

Spectroradiometer (MODIS) products offer a favorable balance of spatial resolution (500 m),

temporal frequency (daily), and long-term availability from both Terra and Aqua satellites

(launched in 1999 and 2002, respectively), making them particularly useful for assessing lake ice

conditions relevant to animal movement. However, many existing related applications of MODIS

rely on manual interpretation of imagery (Pavelsky and Smith 2004; Cooley and Pavelsky 2016)

or simplify spatially complex ice patterns into single metrics, such as average reflectance or

centroid values (Šmejkalová et al. 2016), thereby obscuring the patchiness and progression of

melting that animals likely perceive and respond to. Capturing these within-lake spatial

heterogeneities is essential to link remotely sensed environmental change with fine-scale animal

behavioral responses during migration.

Here we address these gaps by integrating high-frequency GPS tracking of caribou with a

pixel-level albedo analysis derived from MODIS daily surface reflectance data from both Terra

and Aqua satellites. This approach uniquely combines fine spatial resolution with daily updates,

allowing us to quantify dynamic ice conditions at the scale animals actually perceive. Focusing on

the Contwoyto Lake region of Nunavut, Canada, we examine how daily shifts in lake surface

reflectance, as a proxy for ice condition, influence caribou water-crossing behavior. Our results

reveal seasonal behavioral thresholds tied to ice melt and demonstrate how Arctic warming may

erode traditional migratory corridors. This study offers a rare, mechanistic link between climate-

sensitive landscape dynamics and fine-scale migratory decisions.

2. Materials and Methods

2.1 Study Area

Contwoyto Lake (65° 39' 0" N, 110° 43' 0" W) is a large (around 957 km^2 or 369 sq mi) remote Arctic lake, near the border between Nunavut and the Northwest Territories, Canada (Pienitz et al. 1997). The lake is more than 110 km long but no wider than 10 km, with a northwest-to-southeast orientation. The region is characterized by a tundra climate, with long, harsh winters (often below -30°C) and short, cool summers (average 10°C) (Government of the Northwest Territories Department of Transportation et al. 1999). Annual precipitation is low (200–250 mm), with roughly half falling as snow (De Beers Canada Inc. 2002). The area is underlain by continuous permafrost and is located north of the continental treeline. Vegetation is dominated by sedges, dwarf shrubs, mosses, and lichens typical of Low Arctic tundra ecosystems (Downing et al. 2012). Caribou from the Bathurst, Beverly, and Bluenose East herds regularly migrate across or around the lake (Figure 1). In spring, the lake lies directly along the highly endangered Bathurst herd's route between wintering areas to the southwest and calving grounds to the northeast (Gunn et al. 2001), making it a recurrent and functionally important decision point in seasonal migration. In the Tłįchǫ Dene language, the term Kokèti Ekwǫ̀ ("*migratory caribou of Contwoyto Lake*") highlights the deep cultural and ecological ties between Indigenous peoples and the region (Tłįchǫ Research and Training Institute 2018).

Figure 1. *Location of the study area (Contwoyto Lake) in North America. The inset map in the*

bottom left corner of the left panel highlights Canada (in dark grey) within the broader context of

North America. The left panel displays the historical migration ranges (2001–2021) of caribou

herds who use areas around Contwoyto Lake: Bluenose East (blue), Bathurst (pink) and Beverly

(green). These ranges are based on GPS tracking data from 406 individual barren-ground caribou

*(*Rangifer tarandus spp.*) The right panel highlights Contwoyto Lake, shown in the white area based*

on satellite imagery.

2.2 Animal Movement Data

We analyzed GPS tracking data from 406 adult barren-ground caribou whose movements

occurred within 50 km of Contwoyto Lake between 2001 and 2021. The collars were deployed by

the Government of the Northwest Territories' Department of Environment and Climate Change

(GNWT ECC) as part of ongoing population monitoring (Government of the Northwest Territories

2019). The dataset includes individual attributes such as sex, herd affiliation, unique ID, study site,

timestamp, and geographic coordinates (longitude and latitude).

GPS fix rates varied both within and among individuals, ranging from 1-minute to 5-day

intervals. Most data were collected at 8-hour intervals, with some 1-hour fixes triggered when

animals entered geofenced zones around mining infrastructure. Occasional data gaps of up to one

year were observed, likely due to signal loss or collar malfunction. Because our analysis focuses

on the spatial interactions with lake ice conditions at fine temporal scales, we retained the original

fix rates and did not filter or resample the data to preserve temporal heterogeneity and avoid

introducing bias or loss of behavioral resolution.

2.3 Environmental Remote Sensing Data

We used two MODIS remote sensing products to characterize environmental conditions

relevant to caribou movement and lake ice dynamics: (1) the MODIS Albedo Model

(MCD43A3.061) and (2) the MODIS Land Cover Type product (MCD12Q1.061), both at 500 m

resolution. The MCD43A3 Version 6.1 product provides daily estimates of shortwave broadband

black-sky albedo (directional hemispherical reflectance) using 16-day composite data from both

Terra and Aqua satellites from 2000 to 2023, offering the highest quality available for surface

reflectance in high-latitude regions (Schaaf et al. 2011). However, due to polar night and low solar

angle, albedo estimates between mid-October and late March are often unreliable. We therefore

limited our analysis to the 92nd to the 280th day of the year (April 2 to October 7), when high-

quality data are available (Appendix S1: Figure S1). Despite this limitation, the majority of the fall

caribou migration near Contwoyto Lake is completed before October 7, ensuring that the

methodology remains robust during the study period.

To identify lake boundaries, we extracted "pure water" pixels using the International

Geosphere-Biosphere Programme - Data and Information System (IGBP-DIS) land cover

classification (Loveland and Belward 1997; Belward et al. 1999; Sulla-Menashe and Friedl 2019)

within the MCD12Q1.061 land cover dataset. This product provides annual global land cover types,

with associated confidence assessments and quality control metrics from 2001 to 2021 (Sulla-

Menashe and Friedl 2019). We adopted a multi-lake approach based on MODIS-derived pure

water pixels rather than relying on administrative lake boundaries. This approach ensures that all

remotely sensed variables used in our models, particularly albedo, are grounded in ecologically

meaningful, observation-based definitions of lake surfaces. Methodological details and validation

are provided in Appendix S1: Sections 3 and 4.

2.4 Processing Albedo Data

We use surface shortwave albedo as a proxy for lake ice conditions, leveraging its strong

sensitivity to freeze-thaw transitions (Lucht et al. 2000). Albedo values are highest when lake ice

is snow-covered and decrease sharply as ice melts and open water emerges (Appendix S1: Section

5). To address data gaps due to cloud cover or sensor issues, we applied a gap-filling approach

using a Kalman filter with spatial-temporal interpolation, following established climatological

techniques (Welch and Bishop 1995; Jia et al. 2021; 2023; Appendix S1: Sections 6-8). These

preprocessing ensured complete daily albedo time series for each pure water pixel of the lake

across all study years.

To quantify the progression of ice melting and freezing, we defined the "Albedo Percentile

Rank" (APR) for each pixel on each day of a given year as the proportion of all albedo values

observed at that pixel in that year that were less than or equal to the albedo value on that day. This

index dynamically reflects a pixel's position within its own annual albedo range, bounded by its

year-specific maximum (assumed fully frozen) and minimum (assumed ice-free) values.

Calculated in this way, APR is a localized interannually standardized metric that captures

continuous variation in ice conditions along the frozen-to-melted spectrum. For example, an APR

of 90% indicates that the day's albedo is higher than 90% of that pixel's values in that year,

corresponding to an early stage of melting. We relied on this spatially localized and year-specific

measure because the extremal albedo values can vary widely both among pixels within years, and

among years for a given pixel as a function of local environmental features, such as lake depth and

bottom topography. The use of APR does not imply that caribou respond to relative percentiles.

Rather, APR provides a consistent, pixel-specific way to align each year's ice conditions along a

comparable frozen-to-melted progression, especially when absolute albedo values are influenced

by surface wetness and strong interannual variability.

2.5 Processing Movement Data

To investigate how ice conditions affect caribou water-crossing behavior, we classified

movement events near Contwoyto Lake into 3 categories: "Crossing Events", "Circumnavigating

Events", and "Unknown Events". These classifications were based on GPS locations and their

spatial relationship to lake boundaries defined by MODIS-derived "pure water" pixels. "Crossing

Events" were identified when at least one GPS fix from an individual's track fell within the lake

surface boundaries. These cases were treated as confirmed crossings, either over ice or open water,

depending on season and ice conditions. "Circumnavigating Events" occurred when an

individual's track fell within the general vicinity of the lake and intersected with the virtual median

line of the lake's long axis, but no GPS points or interpolated segments crossed into the lake

boundaries. We interpreted these as individuals went around the lake without crossing it.

"Unknown Events" were more ambiguous. These included cases where no GPS fix was recorded

that occurred within the lake itself, but the line segments connecting consecutive GPS points did

intersect the lake boundaries. Each classification was manually verified to reduce misclassification

due to lake shape complexity or GPS error. Information regarding the number of events across

different GPS fix intervals and the influence of temporal resolution on classification uncertainty is

provided in Appendix S3: Section 1.

For each "Unknown Event", we reconstructed two potential movement routes (Figure 2)

across Contwoyto Lake: (1) a "Direct Path" defined as the shortest straight-line route between two

consecutive GPS locations on opposite shores, and (2) a "Circumnavigate Path," defined as the

shortest overland route between the same points that avoids all open water. To further

contextualize the decision, we extracted a "Reference Path," consisting of the three on-land steps

before and after the transit event, to estimate baseline movement behavior. All Circumnavigate

Paths were generated using the *gdistance* R package (van Etten 2017), which applies a raster-based

implementation of Dijkstra's algorithm to approximate least-cost overland routes (Adriaensen et

al. 2003; Etherington 2016). Because space is discretized, these paths represent close

approximations rather than mathematically exact shortest paths. However, at the spatial resolution

and extent of our analysis, this approximation is sufficient for characterizing relative

circumnavigation costs (see Appendix S2). We derived three types of average speeds for each path

("Direct Speed", "Circumnavigate Speed", "Reference Speed") due to varied GPS fix rates.

Additional details on the classification of transit events, least cost path modeling, and path

construction appear in Appendix S2, and full definitions of speed in Appendix S3: Section 2-3.

Figure 2. *The direct path (yellow) and circumnavigate path (red) with the shortest distance between two consecutive starting and ending points (white) on the opposite side of the pure water areas of the Contwoyto Lake (dark grey) for one Unknown transit event (ID 'bat106' in 2012, around 2012-05-14 15:00:00) and the reference path (blue) shows 3 steps before and after the crossing.*

To classify each "Unknown Event" as either a crossing or circumnavigating event, we trained two classification models, Random Forest (RF) and Binomial Logistic (BL) models, using "Crossing Events" and "Circumnavigating Events" as labeled training data (Venables and Ripley 2002; Breiman 2001). These models incorporated ten predictor variables. Unless otherwise stated, all ice-related predictors described below use albedo percentile rank (APR), rather than absolute albedo values. Specifically, predictors spanned movement dynamics (Circumnavigate Speed / Reference Speed, Direct Speed / Reference Speed, and Circumnavigate Speed / Direct Speed), ice

conditions at three spatial scales (APR at the Nearest Pixel, APR Along the Potential Crossing

Path, and APR of the Entire Lake Area), lake features (Lake Width, Proportion of Time Spent in

the Lake Area), and individual traits (Sex, Migration Season) (see Appendix S3: Section 4).

Migration season was defined based on observed movement patterns, with "Spring Migration"

occurring before July 1st, whereas "Fall Migration" occurred afterward.

Because caribou movement characteristics differ markedly between spring and fall

migration periods, we first conducted season-specific analyses by dividing the "Unknown Event"

dataset into a "Spring Only" and a "Fall Only" subset. However, event types were unevenly

distributed between these seasons, with "Crossing Events" dominating in spring and

"Circumnavigating Events" dominating in fall, resulting in opposite forms of class imbalance in

the seasonal datasets. To complement the season-specific analyses and mitigate these imbalances,

we additionally constructed a "Combined" dataset that pooled events from both spring and fall

migrations. This combined dataset provided a more balanced representation of event types and

allowed us to evaluate whether predictors identified in seasonal analyses retained explanatory

power when analyzed jointly.

For each dataset, 80% of the known events were randomly selected for model training, and

the remaining 20% were reserved for testing. Model performance was evaluated using multiple

metrics, including Accuracy, Sensitivity, F1 score, Cohen's Kappa, and Area Under the Receiver

Operating Characteristic Curve (AUC). For RF models, out-of-bag (OOB) error was recorded,

whereas model selection for BL models was based on the delta Akaike Information Criterion

(ΔAIC) (Appendix S3: Section 5). All predicted Unknown Events were labeled as "Crossing" or

"Circumnavigating" based on a 50% predicted probability threshold. Prediction consistency

between RF and BL models was quantified using confusion matrices, representing the proportion

of unknown events that received the same classification from both models.

To mitigate seasonal imbalance in event types (e.g., more crossing events in spring, more

circumnavigating events in fall), we applied cost-sensitive weighting in the RF model (see details

in Appendix S3: Section 6), and variable importance was measured by the Gini Importance Index.

For the BL model, we applied Lasso regression (the *glmnet* R package) to penalize and exclude

redundant predictors. Multicollinearity was assessed using Variance Inflation Factors (VIF), and

redundant variables were removed when VIF > 5. After confirming the final predictors, we used

binned residual plots to assess linearity and introduced quadratic terms only when U- or inverted

U-shaped patterns were evident. Final selection was based on the best converged model with the

lowest AIC using the *dredge* function (the *MuMIn* R package), retaining only predictors with P

value < 0.05 as determined by the *glm* function (the *stats* R package). Model accuracy and

classification were assessed using confusion matrices generated by the *confusionMatrix()* function

from the *caret* R package and from the *randomForest* R package. ROC curves and AUC values

were calculated using the *pROC* package to evaluate the models' ability to discriminate between

crossing and circumnavigating events.

3. Results

We reconstructed seasonal lake ice dynamics using MODIS-derived albedo data for pure

water bodies in Contwoyto Lake. Data gaps were filled using temporal-spatial interpolation with

climatology and a Kalman filter (Figure 3A), ensuring continuous annual coverage outside of polar

night periods. APRs across the lake showed a clear seasonal pattern (e.g., in 2019; Figure 3C):

values decreased from April (dark red), reached a minimum around September (dark blue), and

then increased again by early October (light blue), reflecting the sequential process of ice melt

followed by refreezing in the lake-wide average albedo trend (Figure 3B). To further characterize

spatial variation in ice phenology, we identified the first day each year that pixel-level albedo

reached defined percentiles between its annual maximum and minimum. This provided spatially

explicit estimates of ice melt and freeze timing during the spring and fall migration seasons (see

Appendix S4: Figure S1-S3)

In total, we identified 367 transit events from 130 individuals, all occurring between 2005

and 2021. Of these, 145 occurred during spring migration and 222 during fall migration. In spring

migration, 72 cases were classified as known events (59 crossing, 13 circumnavigating), and 73

cases were classified as unknown. In fall migration, 97 cases were known events (3 crossing, 94

circumnavigating), and 125 were unknown (see Table 1)

Figure 3. *Processing of the albedo data. (A) Albedo of Contwoyto Lake on the 92nd day (April 2nd) in 2019 after preprocessing. Data gaps were filled using temporal-spatial interpolation with climatology and a Kalman filter, and pure water bodies were extracted using land cover data. (B) Average Albedo Percentile Rank (APR) of the lake from April 2nd (92nd day) to October 7th (280th day) in 2019. (C) Spatial distribution of Albedo Percentile Rank (APR) for pure water body pixels from April 2nd (dark blue) to October 7th (dark red) in 2019.*

330   **Table 1.** Distribution of caribou transit events across Contwoyto Lake by event type and migration season (2005–2021), illustrating

331   both seasonal patterns and interannual variability in water-crossing behavior, potentially shaped by behavioral plasticity or limitations

332   in detection.

Migration Season	Transit Event	2005	2007	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	Total for Event	Total for Season
Spring Migration	Crossing Event	1	1			1				4		13	2	13	9	15	59	145
	Circumnavigating Event											4	1	3	2	3	13	
	Unknown Event				2	6	6	4	7	4	12	8	2	12	7	3	73	
Fall Migration	Crossing Event													2		1	3	222
	Circumnavigating Event	2		4	2	1		4		1		5	19	2	38	16	94	
	Unknown Event				2	7	2		4	16	35	28	4	11	10	6	125	

Figure 4. *Spatial Distribution of Caribou trajectories for known events (2001–2021). Event Types:*

Crossing (A, B, E, F), Circumnavigating (C, D, G, H), during spring (A—D) and fall (E—H)

migrations. Spring Migration: (A, B) 59 crossing events; (C, D) 13 circumnavigating events. Fall

Migration: (E, F) 3 crossing events; (G, H) 94 circumnavigating. (A, C, E, G) shows direct paths

of transit events with the starting (yellow) and ending (orange) points, with steps before/after

transit shown from -3 (dark blue) to +3 (dark red). (B, D, F, H) shows trajectories of the transit

events (white).

<u>Crossing Events</u>

A total of 109 GPS relocations from 47 individuals occurred within the boundaries of

Contwoyto Lake. These relocations were unevenly distributed, with more events observed during

spring migration. Summary statistics, including crossing dates, average APR on the day of crossing,

and landscape type where the relocations were located (i.e., lake water or lake island), are

presented in the Appendix S4: Figure S4. During spring migration, direct crossing paths showed a

consistent southwest-to-northeast orientation (Figure 4A, B). In contrast, only a few crossing

events were recorded in fall migration (Figure 4E, F). These fall events featured narrower and

more variable trajectories, reflecting a more spatially constrained and possibly more cautious

movement pattern.

<u>Circumnavigating Events</u>

Using a 20 km buffer around Contwoyto Lake, we identified 13 circumnavigating events

from 12 individuals during spring migration. These events lasted between 2 and 40 days, with

potential cross-lake distances ranging from 0.33 to 29.3 km. In fall, 94 circumnavigating events

were recorded from 57 individuals with durations between 0.16 and 65 days and the potential

cross-lake distances from 0.93 to 47.9 km. In spring migration, circumnavigating routes were

distributed throughout the lake: 5 individuals bypassed the northern portion, 4 the central region,

and 4 the southern part (Figure 5C, D). Most of these paths were west-to-east, similar to the pattern

observed in crossing events. In contrast, fall migration exhibited more frequent and spatially

diverse circumnavigations (Figure 5G, H), with less directional consistency compared to spring

(Figure 5C).

Unknown Events

A total of 73 unknown events were identified in spring migration and 125 during fall

migration. In spring, nearly all direct paths followed a southwest-to-northeast direction (Figure

5A). In fall, however, direct paths showed more diverse orientations and were often aligned with

or parallel to the lakeshore (Figure 5B).

Figure 5. Spatial Distribution of Caribou trajectories for 198 unknown events (2001–2021). (A)

Spring migration (73 unknown events); (B) Fall migration (125 unknown events). Both show direct

paths of transit events with the starting (yellow) and ending (orange) points, with steps before/after

transit shown from -3 (dark blue) to +3 (dark red).

Comparing the most important variables in RF and BL models, "APR Along the Potential

Crossing Path" consistently appeared as a key factor in the "Spring Only" dataset, underscoring

the critical role of ice conditions in shaping water-crossing behavior when lakes are not fully

thawed in spring migration, before July 1st. In contrast, during fall migration, when the lake ice is

almost ice-free, albedo loses its predictive value. Instead, movement-related metrics, such as speed

ratios and the proportion of time spent in lake areas, became dominant. Notably, in the "Combined"

Dataset, albedo regained importance alongside movement dynamics, suggesting that ice conditions

and behavioral flexibility jointly influence caribou crossing decisions. Detailed analysis

supporting these findings are discussed below.

In the "Spring Only" dataset, both the RF and BL models demonstrated high classification

accuracy. The RF model achieved perfect performance on the test data (Accuracy = 1.00; 95% CI:

0.782–1.00; Kappa = 1.00; F1 = 1.00), with a low OOB error. According to the Gini Importance

Index (Figure 6A), the top three predictors were: (1) APR Along the Potential Crossing Path

(medium scale), (2) The Ratio of Circumnavigate Speeds Over Direct Speeds (log), and (3) The

Ratio of Circumnavigate Speeds Over Reference Speeds (log). The best-performing BL model

retained "APR Along the Potential Crossing Path" as the only significant predictor (β = 43.24, SE

= 21.29, P = 0.0422). Predicted crossing probability increased with albedo, with a 50% crossing

probability corresponding to an albedo percentile rank of 0.56 (Figure 6B).

In the "Fall Only" dataset, model performance was affected by extreme class imbalance (3

crossings vs. 94 circumnavigating events). Although the RF model achieved high overall accuracy

(95%, 95% CI: 0.75–0.99), it failed to correctly identify any crossing events (Sensitivity = 0, F1 =

NA, Kappa = 0), highlighting the limitations of the model under skewed data (Table 2). The BL

model performed relatively better, correctly identifying some crossing events (Sensitivity =

66.67%). In this dataset, the most influential predictor in the BL model was "The Ratio of the

Circumnavigate Speeds Over Reference Speeds" (β = 2.6239, SE = 0.9725, P = 0.00694), with

predicted crossing probability exceeding 50% when this ratio surpassed 2.698 (Appendix S5:

Figure S1B). No albedo-related variables ranked among the top predictors in either model.

Table 2. Comparison of model performance and key predictors for classifying caribou lake crossing behavior in "Spring Only", "Fall

Only", and "Combined" datasets.

Model	Most Important Variables in Classification	Prediction Consistency	Accuracy (Test Data)	Sensitivity	F1 Score	Kappa	AUC	delta AIC	OOB error
RF (Spring)	APR Along the Potential Crossing Path	100%	100%	100%	1	1	1	/	3.51 %
	Circumnavigate Speeds/Direct Speeds (log)								
	Circumnavigate Speeds/Reference Speeds (log)								
BL (Spring)	APR Along the Potential Crossing Path		95.80%	96.61%	0.97	0.86	0.99	-0.51	/
RF (Fall)	Direct Speeds/Reference Speeds (log)	98.40%	95%	0%	NA	0	0.94	/	0%
	Circumnavigate Speeds/Reference Speeds (log)								
	Proportion of Time Spent in Lake Area								
BL (Fall)	Circumnavigate Speeds/Reference Speeds (log)		97.94%	66.67%	0.67	0.66	0.99	-0.75	/
RF (Combined)	APR Along the Potential Crossing Path	70.71%	91.18%	86.67%	0.90	0.82	0.99	/	1.48%
	APR at the Nearest Pixel								
	APR of the Entire Lake Area								
BL (Combined)	APR Along the Potential Crossing Path		98.82%	98.39%	0.98	0.97	0.99	-2.12	/
	Proportion of Time Spent in Lake Area								
	Circumnavigate Speeds/Reference Speeds (log)								

404   *Note: Variables listed for RF models represent the top three predictors ranked by Gini Importance Index. P-values are not available*

405   *for RF models. Variables listed for BL models are statistically significant (P < 0.05) and come from the best-converged model selected*

406   *based on the lowest AIC. Abbreviations: RF = Random Forest Model, BL = Binomial Logistic Model, AUC = Area Under the Curve,*

407   *delta AIC = Delta Akaike Information Criterion, OOB error = Out-of-Bag error.*

Figure 6. *Model fitting results for the Random Forest (RF) and Binomial Logistic (BL) models in*

the "Spring Only" dataset. (A) Gini Importance Index (also called Mean Decrease Gini Score)

from the RF model classifying spring transit events (crossing vs. circumnavigating). (B) BL model

showing crossing probability increasing with higher APR along potential crossing paths (blue line

with 95% CI in grey), trained on Crossing (green points) and Circumnavigating Events (red

points). Both models (RF results in purple points, BL results in yellow points) predicted crossing

probabilities above 50% for Unknown Events, indicating strong agreement in classifying caribou

water crossing behaviors during spring migration.

The "Combined" dataset, which integrates both spring and fall events, yielded strong

model performance for both approaches. The RF model achieved 91.2% accuracy on the test data

(95% CI: 0.76–0.98), outperforming the No Information Rate (P = 1.9e–06). The three most

influential predictors were all albedo-related: "APR Along the Potential Crossing Path", "APR at

the Nearest Pixel", and "APR of the Entire Lake Area" (Appendix S5: Figure S1C). The best BL

model achieved 98.8% accuracy and identified three significant predictors: "APR Along the

Potential Crossing Path" (β = 13.78, SE = 3.98, P < 0.001), "Proportion of Time Spent in Lake

Area" (β = 19.63, SE = 9.95, P = 0.049) and "The Ratio of Circumnavigate Speeds Over Reference

Speeds (log)"(β = 1.83, SE = 0.83, P = 0.027). Three crossing events in the "Combined" dataset

occurred at low values of "APR Along the Potential Crossing Path" (with percentile rank < 0.46),

all of which occurred during fall migration (Appendix S5: Figure S1D).

Prediction consistency between RF and BL models varied across datasets. In the "Spring

Only" dataset, both models classified all 73 "Unknown Events" as crossings. "Fall Only" dataset

showed 98.4% agreement, with most "Unknown Events" predicted as circumnavigating,

consistent with the rarity of fall crossing events in this dataset. In the "Combined" dataset,

agreement decreased to 70.7%, with disagreements primarily driven by seasonal differences in

predictor influence. Detailed model results are provided in Appendix S5: Sections 1-3.

To provide system-level climatic context for the behaviorally derived threshold identified

in the spring-only BL model, we quantified interannual variability in lake-wide, pixel-level 56th-

percentile albedo values and identified the timing at which each pixel's albedo percentile rank

(APR) first dropped below its annual 56th percentile during the spring melt-down period each year

from 2005 to 2021 (Appendix S6: Figure S1, Table S1). Neither the annual 56th percentile albedo

value nor the timing of this threshold exhibited a strong monotonic temporal trend. Linear trend

analyses detected statistically significant but ecologically negligible shifts, corresponding to

changes of less than half a day over the study period, with "Year" explaining less than 1% of the

total variance in both albedo values and threshold-crossing timing ($R^2 < 0.01$). Instead, ice

conditions relative to the behavioral threshold were dominated by pronounced interannual

variability. When "Year" was treated as a categorical factor, models explained 65% of the variance

in albedo values and 12% of the variance in threshold-crossing timing. Certain years reached

threshold conditions substantially earlier than others (e.g., 2018), whereas late-threshold years (e.g.,

2020) exhibited delayed transitions. Together, these results suggest that, over the 2005–2021 study

period, variation in lake ice conditions surrounding the behaviorally derived albedo threshold was

expressed primarily through strong interannual volatility, with little evidence for a monotonic

long-term trend (see Appendix S6 for details).

4. Discussion

By aggregating 20 years of GPS tracking data with daily MODIS albedo observation, we

developed a novel, scalable framework linking seasonal lake ice conditions to caribou water-

crossing behavior. Our results reveal a clear seasonal shift in behavioral drivers: in spring, surface

albedo, as a proxy for ice condition, best predicted crossing behavior, while in fall, movement-

based metrics became more influential, indicating that open water poses a greater barrier. These

findings underscore how dynamic surface conditions act as seasonal behavioral filters that shape

migratory strategies, offering mechanistic insights into species' responses to climate-driven

disruptions in landscape connectivity.

4.1 Using Albedo as an Indicator of Ice Condition

We developed a novel approach to quantify lake ice dynamics using MODIS-derived

albedo, offering a rare combination of spatial resolution (500m), daily temporal frequency, and

two decades of historical coverage. The method captures pixel-level freezing and melting patterns

across large Arctic lakes and aligns seamlessly with long-term high-frequency caribou GPS data,

enabling fine-scale behavioral inference across both space and time. By using surface albedo as a

proxy for ice conditions, our method overcomes the limitations of sparse in-situ monitoring

(Magnuson et al. 2000; Eklund 1999) and provides essential environmental context for interpreting

individual water-crossing decisions.

Compared to previous remote sensing approaches, our method strikes a critical balance

between spatial, temporal, and historical dimensions. For example, while Leblond et al. (2016)

used 8-day average NDSI, our daily product allows finer temporal alignment with animal

movement. Synthetic Aperture Radar (SAR) based methods (Du et al. 2015; Stonevicius et al.

2022) provide greater spatial detail but suffer from coarse revisit frequency (5-12 days). Giroux-

Bougard (2023) applied the OPEN-ICE algorithm to 30-m fused Sentinel-2 and Landsat7/8

imagery, but this approach is only available post-2013. Other lake ice products, such as the

European Space Agency's Lakes Climate Change Initiative (Crétaux et al. 2022) and Copernicus

Global Land Service (CGLS) Lake Ice Extent (LIE) product (2022) offer daily coverage but at

either coarser resolution (1000m) or over shorter time spans. Passive microwave sensors (Matias

et al. 2024) offer broad coverage but at much coarse resolution (3 km), and lake-point methods

(Šmejkalová et al. 2016) cannot resolve spatial heterogeneity within large lakes, an essential

feature for linking conditions to animal decisions at migration-relevant scales.

In addition to providing improved data alignment, our method contributes to the

standardization of ice condition metrics, an ongoing challenge in lake ice phenology research.

Rather than relying on inconsistent definitions of "freeze" or "break-up" dates, we introduce a

continuous, percentile-based metric derived from each pixel's annual albedo range. This allows

for a more nuanced characterization of ice transitions and accommodates spatial variability caused

by lake depth, bathymetry, and microclimatic factors. Importantly, during spring melt, surface

albedo can decline rapidly due to wet snow, slush, or meltwater films (e.g., melt ponds; Perovich

et al. 2002; Warren 2019) while ice remains continuous and load-bearing. Under these conditions,

absolute albedo becomes a poor indicator of functional permeability. By employing a pixel-

specific, within-year normalization, the APR metric helps align ice conditions along a comparable

frozen-to-melted progression, reducing interannual variability driven by surface moisture,

illumination geometry, and sensor-related effects. Unlike thresholding approaches that classify

binary ice-water states (Pavelsky et al. 2004; Cooley et al. 2016), our method retains pixel-level

details across the lake surface, enhancing alignment with fine-scale animal movement and

supporting behavioral modeling at intermediate spatial scales. Moreover, by tracking percentile

shifts across years, this framework facilitates long-term monitoring of melt/freeze directionality

and its implications for behavioral plasticity under climate change.

Despite these advantages, our method is constrained by Arctic-specific limitations inherent

to optical remote sensing. MODIS albedo data are only reliable from April to early October (days

92–280), due to low solar angle and polar night conditions, limiting our ability to analyze late fall

freeze-up. Additionally, while surface albedo is an effective proxy for ice conditions, it does not

directly capture ice thickness or load-bearing capacity, which may ultimately determine crossing

feasibility. The 500-m spatial resolution, though adequate for general spatial patterns, may

overlook small-scale heterogeneity near lake edges or in narrow inlets that influence individual

movement decisions. These constraints necessitated the exclusion of certain late-season events and

limited our analysis of fall migration. Future improvements may involve integrating optical and

active microwave (e.g., SAR) remote sensing, combined with machine learning approaches

(Murfitt and Duguay 2021), to enhance spatial and temporal resolution across broader timeframes.

4.2 Water Crossing Behavior

Our results reveal how caribou adjust migratory behavior in response to lake ice conditions,

with particularly strong signals in spring. Surface albedo, used as a proxy for ice condition, was

the most influential predictor of crossing decisions. We identified a clear behavioral threshold:

when APR along the crossing path exceeded the 56th percentile, caribou were more likely to cross

than circumnavigate. Crossing probability rose to 70% at the 60th percentile and reached ~90% at

the 63rd percentile, while it dropped to 10% at the 51st percentile. This quantifiable threshold

offers rare evidence of fine-scale environmental cues driving migratory decisions.

In contrast, fall migration patterns were shaped primarily by the presence of open water. In

the absence of lake ice, caribou relied on movement-based metrics, particularly the log-

transformed ratio of circumnavigate speeds over reference speeds. This shift in behavioral drivers

corresponded to a dramatic seasonal transition: crossing events dropped from 82% of spring

observations to just 3% in fall, while circumnavigating events increased from 18% to 97%. These

patterns underscore the role of lake ice as a seasonal enabler of movement and the extent to which

open water poses as a behavioral barrier to caribou (Leblond et al. 2016; Leclerc et al. 2021).

Notably, we identified three fall migration events ("bat244", "bat292", and "bat205")

likely involving caribou swimming across open water. These events occurred at narrow lake

segments, likely traditional crossing corridors (Williams and Gunn 1982; Gordon 1977; 1996;

2003; 2005), and were characterized by low albedo values (<46th percentile) and slower speeds

(~ 0.39 m/s) compared to their spring over-ice crossings (~ 0.50 m/s). The average swimming

distances (~ 1794 m) were consistent with prior field observations, such as a documented 1600 m

swim by a caribou calf in saltwater (Miller 1995). Caribou are known strong swimmers, often

motivated by food opportunities, predator avoidance, or insect harassment (Webber et al. 2021;

Jeffery et al. 2007; Jordan et al. 2010). Even young calves follow their mothers across open water

without hesitation (Skoog 1968). Reported swim speeds can reach 2.68 m/s during escape

(Banfield 1961), suggesting that our observed values likely reflect intentional, slow crossings

through open water rather than panic-driven flights.

Despite strong behavioral patterns, some uncertainty remains in classifying water crossing

events. Our approach relied primarily on spatial analyses of GPS relocations relative to lake

boundaries, complemented by visual inspection of movement trajectories. Without direct field

validation, brief exploratory movements, such as shoreline hesitation, backtracking, or aborted

crossings, may be misclassified. Commercial high-resolution satellite imagery offers a promising

avenue for post hoc validation, potentially revealing movement traces or disturbance patterns

around suspected crossing sites.

Additional uncertainty arises from variability in GPS fix rates. In some years, tracking

occurred at coarse temporal resolutions (e.g., every 24 or even 48 hours), and fixes were

occasionally missing during transit phases, particularly in late spring when ice conditions fluctuate

rapidly. A supplementary analysis of "Unknown" events across GPS fix interval categories

(Appendix S3: Section 1) indicates that coarser temporal resolution is associated with a higher

proportion of unclassified events, suggesting that classification uncertainty is partly driven by

sampling interval rather than behavioral ambiguity per se. We note, however, that GPS fix rates

reflect practical trade-offs related to battery capacity, deployment duration, and collar weight,

which can limit the feasibility of uniformly high-frequency sampling in long-term tracking studies.

These gaps may obscure short crossings or bias the detection of crossing versus circumnavigation

behavior. Nonetheless, the strength and consistency of seasonal patterns in our dataset suggest that

these limitations do not obscure the broader behavioral signal.

Our findings also underscore the broader ecological importance of ice as a facilitator of

migratory connectivity. In other Arctic regions, sea ice similarly serves as a critical bridge for

inter-island (Peary Caribou) and island-mainland (Dolphin-Union) migration (Miller et al. 2005;

Jenkins et al. 2016). These caribou show high site fidelity to specific sea-ice corridors and often

delay movement until stable surfaces form (Poole et al. 2010); early crossing can be fatal (Dumond

et al. 2013). As climate change reduces the duration and reliability of ice cover, caribou may face

higher energetic costs from longer detours (in our parlance, circumnavigating events) and

increased mortality risks, particularly for vulnerable calves (Miller 1995; Miller et al. 2005;

Dumond et al. 2013). This erosion of seasonal bridges may constrain migratory flexibility and

reduce adaptive capacity across Arctic landscapes.

Our results also raise new questions about the spatial and cognitive scales at which caribou

perceive and respond to ice conditions. The superior predictive performance of crossing-path

albedo compared to local (nearest-pixel) or lake-wide (entire lake) measures suggests that caribou

assess environmental conditions at intermediate spatial scales. Prior experience may play a critical

role, with older individuals or pregnant females potentially guiding herds along historically safer

routes (Williams and Gunn 1982). Future research that incorporates individual age, sex, and

memory-based behavior will improve our understanding of how environmental cues and past

experience jointly shape migratory decision-making in complex and variable Arctic landscapes.

4.3 Migration Under Global Climate Change

Arctic warming exemplifies a broader class of climate-driven disruptions to seasonal

connectivity (Post et al. 2009; Serreze and Barry 2011; Zeigler and Fagan 2014), with lake ice

phenology offering a particularly acute case in northern systems. Earlier break-up and later freeze-

up (Adrian et al. 2009; Dibike et al. 2012) have significantly reduced the seasonal permeability of

safe crossing surfaces. These shifts directly affect migratory connectivity in water-rich northern

landscapes (Downing et al. 2006). While prior studies have emphasized the timing of migration

and arrival at calving grounds (Gurarie et al. 2019; Matias et al. 2024), our results provide finer-

grained behavioral insight into how decisions are shaped by climate-sensitive barriers. Specifically,

we identify quantifiable albedo thresholds that predict spring crossings, offering a rare behavioral

indicator of environmental suitability. As such, the proportion of crossing versus circumnavigating

events may serve as a sensitive behavioral indicator of adaptive capacity in response to small-scale

habitat change.

Interpreting these indicators requires accounting for the spatial complexity of the frozen

landscape. Importantly, the timing of lake-wide mean ice melt should not be interpreted as the sole

constraint on migratory decision-making. Contwoyto Lake is a long (>110 km), narrow (<10 km)

northwest–southeast oriented system that spans a significant latitudinal range. Consequently, ice

melt progresses heterogeneously along this gradient. Our pixel-level analysis (Appendix S6:

Figure S1B) reveals that while the lake-wide mean break-up often occurs later (DOY 155–180),

localized ice degradation in specific corridors begins significantly earlier, with the lower tail of the

distribution reaching the 56th percentile threshold as early as DOY 141 (e.g., May 20). Notably,

this onset of localized deterioration aligns closely with the termination of the spring migration

window described by Matias et al. (2024). This suggests that our behavioral metric captures the

functional environmental threshold that likely constrains the end of the migratory period, as

caribou cease crossing when these early-melting zones lose permeability, even if the average lake-

wide ice conditions remain intact. In contrast, a small number of anomalous years (e.g., 2016)

exhibit more spatially extensive early melt conditions, in which earlier threshold crossing occurs

across a broader set of lake regions compared to typical years, resulting in an overall shift toward

earlier timing at the distributional level. These years represent a distinct regime in which early loss

of lake permeability is no longer confined to a limited set of localized corridors, but instead affects

a larger fraction of the lake, potentially compressing or altering the migratory window relative to

typical years.

Beyond this spatial heterogeneity, our system-level analysis at Contwoyto Lake indicates

that, although weak monotonic trends toward earlier threshold timing and lower albedo values are

statistically detectable, the availability of this crossing window is dominated by pronounced

interannual variability rather than a smooth directional shift (Appendix S6). Although long-term

climatic records document a broad trend toward earlier ice break-up across the Arctic (Magnuson

et al. 2000), our 17-year lake-scale analysis shows that, over the duration of this study, and at the

temporal scale experienced by individual caribou, directional warming signals are frequently

obscured by large year-to-year fluctuations. This volatility is further amplified by the near-

perpendicular intersection between spring migration routes and the lake, such that modest shifts in

ice conditions can translate into discrete behavioral outcomes: either a direct crossing or a

substantial circumnavigation. As a result, small differences in the timing or spatial extent of

crossable ice surfaces can produce outsized effects on movement decisions, reinforcing the

primacy of interannual variability over smooth directional trends at the scale relevant to migration.

Against this backdrop of climatic volatility, the albedo thresholds identified here offer a

mechanistic link between environmental conditions and migratory behavior, providing a

framework for linking locally realized ice conditions to migratory decision-making in dynamic

permeability landscapes under climate change.

Repeated adjustments in timing or route in response to such volatility may indicate

resilience, while persistent increases in circumnavigation could reflect constraints. Such

circumnavigation, especially when combined with adverse weather (Collins and Smith 1991; Eira

et al. 2013), may hinder pregnant females' timely arrival at calving grounds (Fancy and White

1987; Duquette 1988; Leclerc et al. 2021), exacerbate calving asynchrony, and reduce calf survival

(Couriot et al. 2023). Monitoring changes in water-crossing behavior, especially as it relates to ice

thresholds, could therefore provide a behavioral lens through which to detect subtle ecological

tipping points before demographic consequences manifest (Adamczewski et al. 2022).

Beyond caribou, many cold-adapted species rely on ephemeral ice corridors to navigate

fragmented northern landscapes. Our framework, though developed for caribou, is broadly

applicable to migratory animals encountering dynamic surface conditions. Across the Arctic,

species such as moose, muskoxen, Arctic foxes, and polar bears respond strongly to the timing and

stability of ice (Pagano et al. 2021; Banfield 1954b). Globally, frozen waterways serve as critical

seasonal corridors or calving refuges for Eurasian wolves (Veenbrink et al. 2026), Mongolian

gazelles (Dejid et al. 2022), and Tibetan antelopes (Cao et al. 2022), underscoring that ice is not

merely a constraint, but a vital and temporally bounded resource embedded in migration strategies

and life histories.

More broadly, our findings demonstrate how temporally dynamic landscape features, such

as ice, function as transient connectivity windows that modulate movement decisions across

species (Zeigler and Fagan 2014). In such systems, plastic behavioral responses (Xu et al. 2021),

and collective navigation mechanisms (Berdahl et al. 2018) often mediate interactions with shifting

environmental barriers. Our approach integrates remotely sensed ice heterogeneity with individual

movement trajectories to offer a transferable tool for detecting when and where functional

connectivity is lost under climate pressure. Together, these insights highlight the potential of using

behavioral thresholds as cross-species indicators of climate vulnerability.

648   By linking fine-scale behavioral thresholds to large-scale patterns of migratory

connectivity and resilience, our study advances a predictive framework for understanding and

managing movement ecology in a warming world (Kubelka et al. 2022). Identifying quantitative

thresholds, such as the albedo level at which ice becomes crossable, not only improves forecasting

of behavior under changing conditions, but also enables the monitoring of species' adaptive limits

(Winkler et al. 2014; Eggeman et al. 2016; Courtemanch et al. 2017; Berg et al. 2019; Davidson

et al. 2020; Xu et al. 2021). Ice no longer functions merely as a static barrier, but as a seasonal

behavioral filter that reshapes functional connectivity across ecosystems (Zeigler and Fagan 2014;

Uroy et al. 2021). As migration corridors fracture under climate pressure, shifts in movement, such

as threshold-based crossings and increasing circumnavigations, may provide early warning signals

of ecological tipping points. This perspective is particularly important for conservation planning

(Kauffman et al. 2021), where the protection of migration corridors must account for both static

structural features and dynamic environmental conditions (Reynolds et al. 2017; Moore and

Schindler 2022). The integration of spatially explicit behavioral models with long-term remote

sensing offers promising tools for anticipating future bottlenecks, guiding the design of adaptive

monitoring systems, and informing cross-species conservation strategies in an era of accelerating

climate instability (Neumann et al. 2015; Lahoz-Monfort and Magrath 2021). By closing the gap

between landscape dynamics and individual movement decisions, our framework advances a

migration ecology that is not only descriptive, but predictive and actionable under global climate

change.

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Animal Care Protocols

684   All animal handling and data collection procedures were conducted in accordance with

685   ethical guidelines and approved by the appropriate institutional animal care and use committees.

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Conflicts of Interest

The authors declare no conflicts of interest related to this study.

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