

## Research



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# Local meteorological conditions reroute a migration

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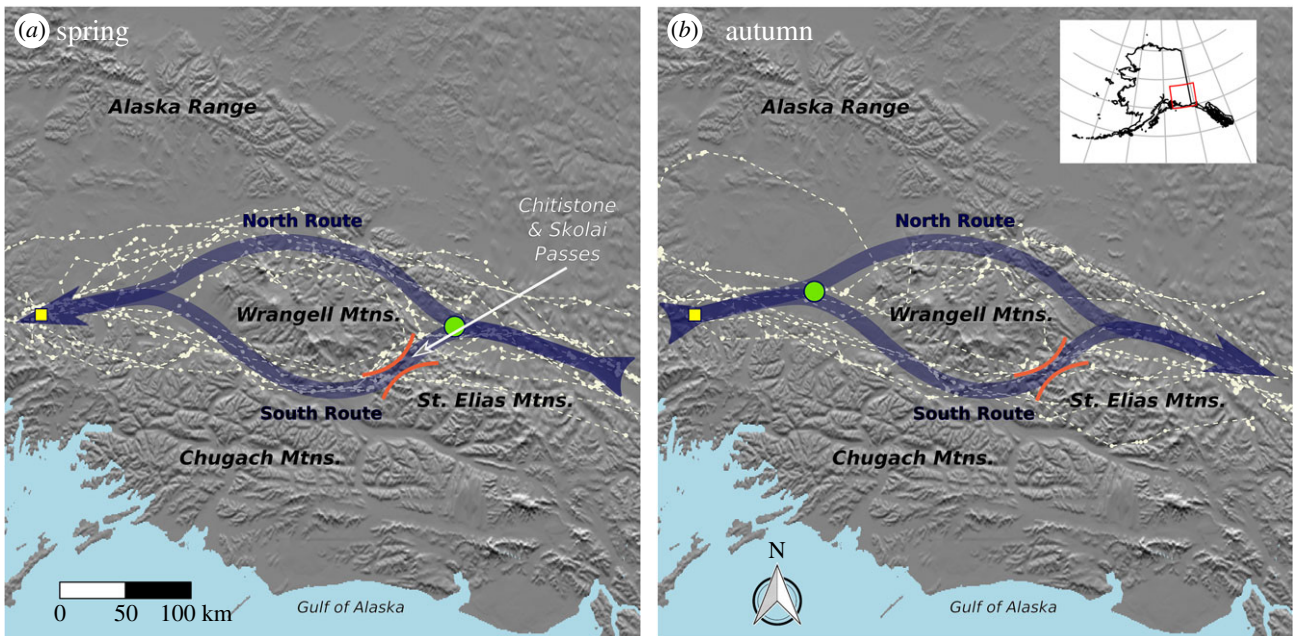
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For migrating animals, realized migration routes and timing emerge from hundreds or thousands of movement decisions made along migration routes. Local weather conditions along migration routes continually influence these decisions, and even relatively small changes in *en route* weather may cumulatively result in major shifts in migration patterns. Here, we analysed satellite tracking data to score a discrete navigation decision by a large migratory bird as it navigated a high-latitude, 5000 m elevation mountain range to understand how those navigational decisions changed under different weather conditions. We showed that wind conditions in particular areas along the migration pathway drove a navigational decision to reroute a migration; conditions encountered predictably resulted in migrants routing either north or south of the mountain range. With abiotic conditions continuing to change globally, simple decisions, such as the one described here, might additively emerge into new, very different migration routes.

## 1. Introduction

Migration routes and strategies strongly affect fitness, and migration corridors provide important connectivity between geographically distant systems [1]. Routes and timing are closely tied to environmental conditions, and timing in particular has been clearly demonstrated to have substantial impacts to fitness [2]. However, migratory behaviour of birds is changing with climate variation [2–5]. Phenological miscuing and disjunction occur when initiation of migration is mistimed due to some cue (e.g. weather) and reproductive stages are poorly aligned with resource availability in breeding areas [6]. Severe miscuing or disjunctions often results in failed breeding attempts and heightens the probability of adult mortality, with commensurate harmful effects to populations [7].

As climate change can alter migratory behaviour [2–5], efforts to understand climate's effects on migration have generally focused on large-scale, cross-sectional or population-level behavioural phenomena, such as phenological miscuing, disjunction and short-stopping [6,8]. These large-scale patterns, however, emerge from many hundreds or thousands of smaller-scale decisions made by individuals along migration routes, each affected by a suite of intrinsic and extrinsic factors that animals experience before and during migration [9]. For example, some individual decisions can be as simple as going one way or another around a particular landscape feature. The effect of local *en route* conditions on these individual decisions can emerge as altered migration behaviour that may or may not respond adaptively to ongoing environmental change [10]. Limited study of fine-scale movement of free-living animals has left us with a poor understanding of movement decisions during migration, how climate-related changes might affect them and how they sum to overall migration patterns at both individual and population levels [9].



**Figure 1.** Relief map of the study area with relevant mountain ranges labelled and golden eagle route choice around the Wrangell Mountains illustrated. Labelled arrows correspond to the approximate direction of migration for the indicated season. Beige points correspond to the discrete GPS locations recorded by the transmitters for 28 example eagle tracks with transmitters on intervals of one to several hours with dashed lines showing linear interpolations between. Green filled circle is the spatial location weather data were interpolated to. Yellow filled square is the location of Gunsight Mountain.

A major area of work in the growing field of movement ecology involves investigating how fine-scale movement decisions interact with intrinsic and extrinsic factors to emerge as an animal's observed movement pattern [9]. Technologies to track animals are advancing rapidly, as are new analytical methods to parse the often rich data streams they create. It is now possible to probe the environmental and physiological processes affecting individual movement decisions that occur during migrations [11,12].

A key aspect of these movement decisions is energy expenditure and efficiency. The movement efficiency of animals migrating through moving fluids, such as birds in the air, can be drastically improved or reduced by changes in ambient conditions and fluid flow [13–15]. Soaring species, including many raptors, are dependent upon upward air motion, such as thermal uplift, for efficient locomotion [13,16]. Constant adjustments in response to conditions in the air column allow an individual to move efficiently by taking advantage of energetic flight subsidies provided by local meteorological phenomena along migration routes [17]. Such reliance on atmospheric conditions directly links movement capacity and the energy landscape to climate-affected environmental variables [9,18]. Changes in climate and weather along migration corridors will affect the efficiency and risk associated with certain migration routes and timing [15]. These effects will also interact with climate-driven landcover change to influence both *en route* weather conditions and food resources. Identifying how weather, such as wind and cloud prevalence, drives individual decisions is, therefore, key to predicting potential shifts in migration routes. Weather is well known to influence aerial migrant decision-making [15,17,19]; however, despite being a source of changes in migration routes, discrete navigation decisions are infrequently addressed in the migration literature [20]. Predicting such shifts in route requires an understanding of how individual navigation decisions are made and could prove important to placing energy

infrastructure, such as wind turbines, that are known to impose increased mortality on wildlife [21].

Here, we examine the movement behaviour of a holarctic, large soaring bird and apex predator, the golden eagle *Aquila chrysaetos*, at a point along a migration corridor to understand how local weather affects a movement decision resulting in a major shift in the realized migration route. Some golden eagles that summer and breed in southcentral Alaska and overwinter at temperate latitudes of western North America make a nearly 4000 km migration biannually, negotiating the highest mountain ranges in North America. Near the Alaska–Canada border in southeastern Alaska, these eagles migrate around the Wrangell and Saint Elias Mountains with peaks over 5000 m and the largest glaciers and ice fields on the continent. Eagles must fly either north of the Wrangell Mountains, or make a meridional shift to a more southern route via 1800 m elevation mountain passes (figure 1).

Understanding that migratory movements of soaring birds are affected by weather, we hypothesized that meteorological conditions proximate to the Wrangell Mountains encountered *en route* would, at least in part, determine the choice of route around the mountain range. We first predicted that cloudier and rainier conditions would affect the navigability of mountain passes by limiting visibility and because the moisture in the air would negatively affect performance of flight feathers, which would make the southern route less favourable. Given the general meridional orientation of the transition between routes, we also expected that velocity of the north-south wind would influence route choice, with headwinds in passes making the south route more energetically demanding and thus less favourable. Also, eagles are known to use orographic uplift as a flight subsidy [17], so uplift generated by wind along each route could make a route energetically favourable. Lastly, thermal uplift is also known to influence flight performance of soaring birds [13,17], so we predicted it could affect this navigation decision such that thermals radiating from south-facing slopes might favour choice of the southern

route, where south-facing slopes would be more abundant and receive greater solar radiation. We also considered that any combination of these hypothesized effects of weather could be additively driving route choice.

## 2. Methods

### (a) Model system

Golden eagles are a large soaring raptor distributed across the Holarctic [22]. While some populations are classified as partially migratory, most individuals that summer and breed above approximately 55°N in North America are true long-distance migrants [22,23]. Golden eagles are predatory and opportunistic, using for food resources many taxa, ranging from small mammals and birds to ungulates, often scavenging carrion [22,23]. Recent observations indicate that golden eagles likely occupy Alaska at high summer densities [24].

Tracking efforts by the Alaska Department of Fish & Game (ADF&G), National Park Service (NPS) and US Fish & Wildlife Service (USFWS) indicate that many of the golden eagles that summer and breed in southwestern and southcentral Alaska use a narrow migration corridor near Gunsight Mountain, Alaska (61.67° N 147.35° W; figure 1). Prior to reaching the corridor in the spring and just after moving through it in the autumn, each individual eagle appears to select a migratory route—north or south—around the Wrangell Mountains. If the southern route is chosen, individuals must fly through 1800 m elevation mountain passes or occasionally at a high altitude over the southern aspect of the Saint Elias Mountains. The northern route requires no movement through such high-elevation terrain and is characterized by foothills and mountains with approximately 700–1000 m valleys and passes. Additionally, neither route is shorter than the other (figure 1), and there is little evidence that either route has obvious advantages independent of weather conditions. Chitstone and Skolai passes, through which eagles fly to take the southern migration route, mark the eastern edge of the Wrangell Mountains and the western edge of the Saint Elias Mountains. The passes descend into the low-elevation (approx. 200–300 m) Chitina River valley between the Wrangell and Chugach Mountains. It is important to note that while this population of eagles migrates between northern breeding grounds and southern overwintering areas, individuals migrate through southeastern/south-central Alaska *east to west* during spring migration and *west to east* during autumn migration (figure 1). Hence, winds along the north–south axis, possibly modified by topography, can offer head-/tailwinds and/or orographic uplift for an eagle while transitioning to the chosen route. We explore the effects of wind and its effect on movement through mountain passes further in the Discussion.

### (b) Data collection

Golden eagles were captured with a remote-fired net launcher placed over carrion bait near Gunsight Mountain. Captures occurred during spring migration from mid-March to mid-April 2014–2016. Eagles were equipped with back pack solar-powered Argos/Global Positioning System (GPS) platform transmitter terminals (PTTs; Microwave Telemetry, Columbia, MD, USA). All eagles were sexually mature, with age estimated as entering their 4th year at capture—though most were greater than 5th year—so we did not consider effects of age [25]. PTTs were programmed to record GPS locations on duty cycles, ranging from 8 to 14 fixes per day during migration (8 hourly, 13 hourly plus midnight or 3 h fixed interval). Short days often resulted in insufficient battery voltage for PTTs to take fixes, so the resulting GPS tracks had missing observations.

During migration, route choice was scored (north or south) based on the individual's latitudinal location between 144.3° W

and 142.3° W longitude, which approximately correspond to the eastern and western edges of the Wrangell Mountains. Timestamps were recorded for the GPS location just prior to reaching those points. In none of the cases was route assignment ambiguous; eagles were either north of the mountain range or south, making it a clear binary decision for migrating individuals. If a tag did not record a complete enough track through the area to determine route, that decision was not scored nor included in the analyses.

Meteorological data were gathered from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis I. Variables were interpolated in latitude, longitude and time trilinearly with R and the package 'RNCEP' [26] from the nearest four spatial points and two temporal times of prediction (2.5° spatial and 6 h temporal resolution). Each decision was assigned the values of environmental variables interpolated from the reanalysis to the surface at 61.744469° N 141.461205° W and 62.108325° N 145.554793° W for spring and autumn migration, respectively, and the timestamp recorded by the transmitter just prior to reaching those areas of route divergence (figure 1). These environmental data are predicted on a much larger scale than how an animal interacts with them at precise points, so our results must be interpreted carefully. The overarching driver of the route choice process is likely the prevailing regional weather conditions, which are larger than the NCEP/NCAR model grid and also influence finer-scale weather, so although a finer model grid might capture more complexity, the weather variables interpolated to the chosen points should be representative of the process. Higher resolution data, in terms of both the movement data and meteorological data, would allow for more precise inferences on details of behaviours and decisions; however, more complex analytical frameworks would be required.

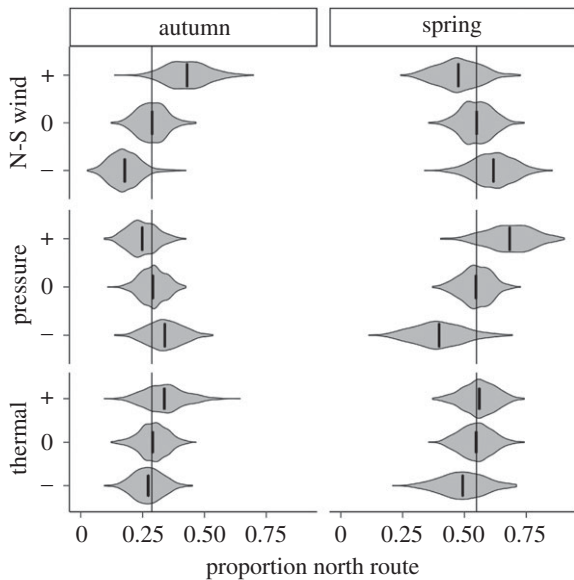
### (c) Analyses

We modelled this binary decision of route choice as a Bernoulli random variable. We used the Bayesian equivalent of a generalized linear model (GLM) with a *logit* link and hierarchical structure to account for effects of an individual. The model was fitted with Hamiltonian Monte Carlo (HMC) in R and Stan using the package 'rstanarm' [27]. This was done with the function 'stan\_glmr', using 20 000 HMC iterations, including 10 000 warm-up, and default weakly informative priors ( $\mathcal{N}(0, 2.5^2)$  on coefficients and  $\mathcal{N}(0, 10^2)$  intercepts). We confirmed model convergence to the posterior distribution with traceplots, Gelman diagnostics, effective sample sizes and posterior plots of parameters [27].

We compared candidate models with leave-one-out cross-validation approximated by Pareto-smoothed importance sampling (PSIS-LOO) in R with the package 'loo' [28,29]. We ranked the models by the expected *log* pointwise predictive density (i.e. out-of-sample predictive accuracy) transformed onto the deviance scale (i.e. looic [29]), which allowed applying the rules of more traditional information-theoretic model selection (e.g.  $\Delta\text{looic} > 2$  to accept model as better fit [30]). Lastly, to assess model fit and illustrate the effects of varying environmental conditions, we sampled from the posterior predictive distribution of the top model with the function 'posterior\_predict' in 'rstanarm.' For models with multiple covariates, posterior predictive draws were done with the other covariate(s) (i.e. those not being visualized) held constant at the empirical values. The empirical data were shifted up or down one standard deviation to observe effects. Posterior predictive draws using the empirical data provided evidence of good model fit and predictive ability (figure 2; electronic supplementary material, S1). R code and the decision data are provided as electronic supplementary material.

### (d) Candidate models

To understand the potential effect of meteorological conditions on how eagles choose a route around the Wrangell Mountains, we



**Figure 2.** Model predictions of effects of meteorological variables on the proportion of 135 eagle decisions resulting in a route north of the Wrangell Mountains. Violins are composed of 1000 posterior predictive draws from top fitting models with vertical bars showing means. Zero indicates posterior predictive draws with observed data—done as a posterior predictive check to confirm the models predict reasonably well—and plus and minus indicate the empirical values + and − one standard deviation, respectively. Vertical lines represent the observed proportions of eagles that chose the north route. N-S wind corresponds to the velocity of the wind from south to north. Distributions right of the observed proportion indicate that variable, if changed, would increase the proportion of eagles choosing the north route.

used four environmental predictor variables. We included barometric pressure as a predictor to capture approaching large-scale weather systems. Weather fronts can approach the area from the Gulf of Alaska, deteriorating conditions along the south route. Blocking high pressure is predominant in Interior Alaska in spring, however, so low pressure could indicate a transition to a progressive pattern, which would make weather along the north route less predictable. Clouds and precipitation could also be caused by local, more stochastic conditions. To capture such a potential effect, we used relative humidity. At 100% humidity, clouds form and precipitation autumn. Note that high humidity at the surface can indicate 100% humidity aloft, resulting in precipitation falling to the surface without air at the surface reaching 100% humidity. Winds can generate flight subsidies (orographic uplift) for eagles as well as turbulence. NCEP provides the zonal and meridional components of wind. We chose to include the meridional component (i.e. velocity of wind from south to north) in models, which would generally correspond to head- or tailwind support during a meridional shift in route. Positive meridional wind corresponds to winds from the south and negative winds from the north. We only used one wind component to avoid collinearity, and initial exploratory data summaries and modelling showed the zonal component to be much more consistent in magnitude and have little to no predictive power. The relatively low resolution of the movement data through the study area due to the programmed duty cycles and missing data did not permit using tailwind as a predictor. Lastly, surface sensible heat flux was used to approximate available thermal uplift, as it is often used to model uplift [31]. We gave day of year careful thought as a predictor, as it could serve as a proxy for physiological changes and/or changes in urgency during migration, and constructed a candidate model set that included it (electronic supplementary material, table S2). Weather makes predictable seasonal progressions, so the addition of day of year into candidate models

imparted collinearity. Additionally, an effect of day of year implies that one route is inherently shorter than the other, independent of weather, for which we do not have evidence. We thus decided not to include it in the final set of candidate models; however, we would like to note that the modelling we did that included day of year did not find it to be a strong predictor of route choice (electronic supplementary material, table S2), despite evidence of its importance to other behavioural aspects of migration [32,33].

Considering our hypothesized meteorological effects, we constructed a set of 30 candidate models, in addition to a null intercept-only model (electronic supplementary material, table S1). These included interactions with season, as we expected weather might have season-specific effects on route choice. As we did not have specific predictions about how certain combinations of variables might drive route choice, our model set was constructed with all possible additive combinations of variables and interactions with season. A north–south wind by season interaction would be expected due to opposing directions of migration between seasons, so we included wind only with a season interaction. All candidate models included a random intercept of individual to account for variability in route preference among individuals. Random slopes were not considered due to small individual-level sample sizes. Empirical meteorological predictor distributions were centred and standardized. Relative humidity is proportional, so we first applied the logistic transform to map it to an unconstrained space. Models with interactions included the main effects of the interacting variables as well. The predictor variables showed some correlation: Barometric pressure and sensible heat flux showed very little correlation ( $r = 0.02$ ), wind and humidity showed the greatest amount of correlation ( $r = 0.65$ ) and the remaining pairwise combinations showed low correlation ( $-0.18 < r < 0.32$ ).

### 3. Results

We identified a route choice for 44 individuals during spring and autumn migrations 2014–2017 (total of 73 autumn and 62 spring individual migrations) and detected the ability to use either the north or south route for half of the 34 eagles tracked through the study area over multiple migrations. Northern routes were used 26% less often in the autumn than spring (table 1), but variability among intercept estimates indicates there was individual-level variability in the probability of choosing the north route (electronic supplementary material, figures S2–S4), indicating that individuals exhibit an inherent preference for one route. Migrants generally encountered stronger winds, higher humidity and greater thermal uplift in the spring than in the autumn (table 1).

The top two performing models provide evidence for effects of wind, season and barometric pressure on the choice of route around the Wrangell Mountains (table 2); the ranking indicates that the wind  $\times$  season model was a negligibly better fit than the model including pressure. The effects of wind were season specific: Stronger winds from south to north in the autumn caused more migrants to use the north route, whereas stronger south to north winds in the spring tended to shift use to the south route (figure 2). The model results indicate an increase in south to north wind of approximately  $2 \text{ m s}^{-1}$  corresponds to approximately 14% more eagles choosing the north route in autumn and approximately 7% fewer in spring, with similar opposite effect sizes for a reduction in south to north wind (table 1 and figure 2; electronic supplementary material, S2). Lastly, a reduction in barometric pressure by approximately 0.01 bar increased use of the

**Table 1.** Proportion of golden eagles tracked that chose a northern migration route around the Wrangell Mountains and the summary statistics of meteorological variables interpolated to the approximate location and time each eagle chose a route. Pooled summaries and summaries specific to route choice are presented. N-S wind is velocity of south to north wind. Negative thermal uplift (surface sensible heat flux) is flux towards the surface.

season	route	proportion	N-S wind	relative humidity	barometric pressure	thermal uplift
		north route	$\text{m s}^{-1}$ (s.d.)	% (s.d.)	Bar (s.d.)	$\text{Wm}^{-2}$ (s.d.)
autumn		0.29	−0.66 (1.88)	76.61 (17.18)	1.011 (0.012)	−29.48 (26.85)
	north		−0.20 (1.68)	81.59 (14.98)	1.007 (0.009)	−24.82 (28.49)
	south		−0.84 (1.94)	74.60 (17.73)	1.012 (0.013)	−31.37 (26.21)
spring		0.55	1.92 (2.23)	90.50 (7.69)	1.008 (0.006)	−3.21 (25.09)
	north		1.61 (1.91)	90.24 (7.97)	1.009 (0.006)	−0.38 (24.61)
	south		2.30 (2.56)	90.81 (7.46)	1.007 (0.006)	−6.65 (25.69)

**Table 2.** Candidate models of route choice around the Wrangell Mountains ranked by leave-one-out cross-validation approximated by Pareto-smoothed importance sampling. Lower information criterion (loaic) indicates better model fit. Top 10 candidate models and null intercept-only model are shown. All models include random intercept for individual. Interaction models include all main effects. Meteorological predictors were interpolated to the approximate location and time each eagle chose a route. 'Wind' is the velocity of south to north wind. Negative thermal uplift (surface sensible heat flux) is flux towards the surface.

model	loaic	$\Delta$ loaic
wind $\times$ season	146.5	0
wind $\times$ season + pressure $\times$ season	148.1	1.6
wind $\times$ season + thermal	148.8	2.3
wind $\times$ season + pressure $\times$ season + thermal	149.2	2.7
wind $\times$ season + pressure	149.4	2.9
pressure $\times$ season	149.5	3.0
wind $\times$ season + humidity	149.9	3.4
wind $\times$ season + thermal $\times$ season	151.0	4.5
pressure $\times$ season + thermal	151.3	4.8
season	151.4	4.9
null	159.7	13.2

southern route in spring by approximately 15% (table 1 and figure 2; electronic supplementary material, S3).

## 4. Discussion

Our results show how local to regional scale meteorological conditions can drive a discrete navigation decision, rerouting a migration. As weather patterns are changing on large scales with climate, it is reasonable to expect choice of migration routes to change. Reduction of the equatorial-polar thermal gradient via climate warming at the poles and anthropogenic increases in surface roughness have reduced wind speeds in North America and globally over the last few decades, with decay expected to continue [34–36]. Even small changes in wind have already been shown to alter ecology and trophic dynamics [37], highlighting the importance of understanding

the effects of wind patterns on ecological and animal decision-making processes, such as annual migration.

The magnitude of the north wind clearly affects an eagle's choice to migrate north or south of the Wrangell Mountains, but uplift dynamics and how wind drives those dynamics are also important. Winds would generate orographic uplift in the form of upslope winds in the foothills along each route. Migrants heading north in the spring migrate along the Wrangell Mountains in a general westbound direction (figure 1), and north winds would generate orographic uplift along the north-facing slopes of the north route. South winds could also generate orographic uplift along south-facing slopes of the south route and key passes in transitioning to the route. Orographic uplift has been shown to be an important energetic subsidy for migrating eagles [17]. In autumn, north winds might offer tailwind support for eagles moving southwest to the south route, and south winds, a tailwind in moving northwest to the north route. Also, strong winds can cause clouds and precipitation along the windward route due to the orographic effect, which could favour use of the leeward route (figure 1). Furthermore, due to the solar trajectory, the more abundant south-facing slopes along the southern slope of the Wrangell Mountains would likely become free of snow earlier, offering additional flight subsidy in the form of thermal uplift and possibly incentive for shifting to the south route in spring [14–17]. Although the top two models were slightly better fits (table 2), the third-ranked model indicates individuals shift to the south route at a higher rate when thermal uplift is more limited in spring (figure 2).

Evidence for weather systems influencing migration timing exists [38]; however, we found evidence that changes in large-scale weather patterns influence migration on scales as fine as discrete route choice (table 2). Blocking high pressure is predominant in springtime interior Alaska, so a transition to a progressive or active weather pattern, signalled by a downward pressure trend, would correspond to much less predictable weather along the north route, probably making it less favourable to migrants. Our top model with barometric pressure predicted a strong effect of changes in pressure on spring route choice (figure 2), consistent with a meteorological progression away from the predominant, favourable conditions along the north route. Weather systems modifying pressure gradients can also shift migration routes due to inherent effects on wind conditions [39].

Changes in migration routes due to individual decisions could additively have large-scale effects. Variable migratory

behaviour can affect energy expenditure [8,40], which can carry over to influence individual survival and reproductive success [41]; these, in turn, can precondition population-level declines [7]. As we have shown, how fine-scale movement decisions emerge into a population-level movement corridors of migrants can be associated with individual preference and variables that will be altered by climate change. Monitoring fine-scale movement decisions of long-distance migrants, in particular, will be crucial as climate change advances, as dynamic conditions will alter decision-making processes and thus likely the basal energy expenditure associated with each possible decision [20]. Animals may be limited to fewer possible routes, or change might make additional routes available. For example, receding glaciers could open avenues of favourable uplift dynamics for soaring migrants in newly ice-free areas. In either case, an animal's decision will be driven, in part, by the environment, and better decisions will increase the chance of safe arrival to breeding areas, improve survival and increase reproductive success [20].

**Ethics.** Field procedures were conducted following the Alaska Department of Fish & Game Animal Care & Use Committee protocol no. 2013-036 and University of Alaska Fairbanks Institutional Animal Care & Use Committee protocol no. 859448.

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