Received: 1 March 2023 | Revised: 22 August 2023 | Accepted: 19 September 2023

DOI: 10.1002/ecy.4196

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

# Going with the floe: Sea-ice movement affects distance and destination during Adélie penguin winter movements

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**Funding information**
National Aeronautics and Space Administration, Grant/Award Number: 80NSSC19K0189; National Science Foundation, Grant/Award Numbers: 1543459, 1543498, 1543541, 1935870; NSF Graduate Research Fellowship Program, Grant/Award Number: 1938055

**Handling Editor:** John P. Arnould

## Abstract

Seasonal migration, driven by shifts in annual climate cycles and resources, is a key part of the life history and ecology of species across taxonomic groups. By influencing the amount of energy needed to move, external forces such as wind and ocean currents are often key drivers of migratory pathways exposing individuals to varying resources, environmental conditions, and competition pressures impacting individual fitness and population dynamics. Although wildlife movements in connection with wind and ocean currents are relatively well understood, movements within sea-ice fields have been much less studied, despite sea ice being an integral part of polar ecology. Adélie penguins (*Pygoscelis adeliae*) in the southern Ross Sea, Antarctica, currently exist at the southernmost edge of their range and undergo the longest (~12,000 km) winter migration known for the species. Within and north of the Ross Sea, the Ross Gyre drives ocean circulation and the large-scale movement of sea ice. We used remotely sensed sea-ice movement data together with geolocation-based penguin movement data to test the hypothesis that penguins use gyre-driven sea-ice movement to aid their migration. We found that penguins traveled greater distances when their movement vectors were aligned with those of sea ice (i.e., ice support) and the amount of ice support received depended on which route a penguin took. We also found that birds that took an eastern route traveled significantly further north in two of the 3 years we examined, coinciding with higher velocities of sea ice in those years. We compare our findings to patterns observed in migrating species that utilize air or water currents for their travel and with other studies showing the importance of ocean/sea-ice circulation patterns to wildlife movement and life history patterns within the Ross Sea. Changes in sea ice may have consequences not only for energy expenditure but, by altering migration and movement pathways, to the ecological interactions that exist in this region.

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*Ecology*. 2024;105:e4196.
https://doi.org/10.1002/ecy.4196

**KEYWORDS**
global location sensors, ice support, migration, migratory pathways, movement ecology, remote sensing, Ross Sea, sea ice, winter ecology

# INTRODUCTION

Seasonal migration, driven by shifts in annual climate cycles and resources, is a key part of the life history and ecology of species across taxonomic groups (Alerstam et al., 2003). While several factors dictate how and where species move, external forces such as wind and ocean currents are often key drivers. These forces shape migrations by influencing the amount of energy needed to move. Indeed, movement pathways have been described as depending on "energy landscapes" which modulate how animals respond and move through heterogeneous environments (Shepard et al., 2013; Somveille et al., 2021). Numerous studies have shown, for example, that birds adjust their flight behavior and routes in response to changes in wind to travel faster and more efficiently (Kranstauber et al., 2015; Spear & Ainley, 1997) and that these patterns hold true across multiple spatiotemporal scales (Weimerskirch et al., 2012).

Different migratory routes expose individuals to varying resources, environmental conditions, competition pressures and ultimately energetic costs and gains (Alves et al., 2013). In addition to driving how and where species move, the energetic cost of migration has been linked to individual survival, breeding productivity, and population dynamics (Fayet et al., 2017; Harrison et al., 2011; Szostek & Becker, 2015). The internal state of an individual (e.g., its motivation, nutritional state, and parasite load), potentially as a carryover effect from breeding season events, can also interact with external factors to shape migration timing and route (Nathan et al., 2008; Oudman et al., 2020). Thus, identifying differences in migratory pathways within and between populations can help highlight ecological constraints and conservation issues shared by one or more populations or, conversely, specific to some fraction of the population.

Although wildlife movements in connection with wind and ocean currents have received considerable attention, movement within sea-ice fields has been much less studied, despite sea ice being an integral part of polar ecology (Massom & Stammerjohn, 2010; Post et al., 2013). Sea ice offers a special case of how fluid type dynamics might affect the long-distance movements and associated costs for birds and mammals as it tends to be very dynamic and fragmented, can serve as both a platform and barrier for migration, and species have evolved behaviors and morphology to adapt (Ainley et al., 2003, 2017). Thus, while there is much that may be understood within the context of flying or swimming migrants, movements on sea ice can provide new insights into migration strategies. Moreover, climate change is disproportionately impacting polar regions, and projected changes to Antarctic winds, ocean currents, and sea ice make it increasingly important to understand how and when wildlife that depend on sea ice for their movements could be affected (A. Clarke & Harris, 2003).

Adélie penguins (*Pygoscelis adeliae*) are a highly mobile key mesopredator within the Southern Ocean marine ecosystem and breeding colonies are widely distributed throughout the Antarctic coast (Lynch & LaRue, 2014). Throughout the year they are closely associated with sea ice for feeding, resting or avoiding predation, and previous studies have suggested that Adélie penguin winter locations and movements could be influenced by sea ice at broad spatiotemporal scales (Ballard et al., 2010; J. Clarke et al., 2003; Takahashi et al., 2018). However, the mechanism for how and when sea-ice circulation patterns might facilitate or constrain their migration, especially at smaller scales, remains unknown. Adélie penguin populations breeding on Ross Island in the southern Ross Sea undergo the longest known migration for the species, traveling over 12,000 km on average (Ballard et al., 2010), providing a unique opportunity to assess the interaction between an upper trophic level species and its dynamic sea-ice environment. Additionally, the populations of the three Ross Island breeding colonies (~15% of the world population) have exhibited different phenologies, over-winter survival rates and, ultimately, trajectories over the past 40 years (Dugger et al., 2010; Lyver et al., 2014) and it has been suggested that intercolony differences in migration strategies could be responsible for part of these differences (Ballard et al., 2010). Extensive interindividual variation has also been shown in these populations, regarding age at first reproduction (Kappes et al., 2021), reproductive success (Lescroël et al., 2009), and foraging strategies (Lescroël et al., 2020), but nothing is known about interindividual differences in migratory behavior. Therefore, understanding how migration strategies and routes could differ between individuals and/or colonies, and how changes in the movement of sea ice may affect these could inform us about the broader ecological consequences of a changing icescape.

As these populations move north they encounter the Ross Gyre, a system of wind and ocean currents driven in part by the Antarctic Circumpolar Current (ACC) which drives the large-scale cyclonic clockwise movement of sea ice throughout much of their wintering range (Kwok et al., 2017; Figure 1). Thus, depending on whether Ross Island Adélie penguins are moving north postbreeding or south prebreeding, or dispersing at their most northern locations during winter, we hypothesize that they would use sea-ice movement at times to travel faster and at lesser costs, the way flying birds use wind. At other times penguins may be hindered by the sea-ice circulation pattern or move with or against it to stay within more productive waters (Tynan, 1998). To test these hypotheses, we used remotely sensed ice movement data, derived from satellite imagery, together with geolocation-based penguin movement data collected across 3 years and two colonies. We predicted that (1) penguins would travel longer distances when their speed and direction aligned with those of sea ice (i.e., ice support), (2) penguins would receive more ice support when they are traveling away from then toward their breeding colony, in conjunction with the cyclonic pattern of the gyre, (3) a higher velocity of the Ross Gyre would result in the northbound penguins being advected farther north and further from their breeding colony, consistent with the large-scale sea-ice extent in the Ross Sea region varying in accord with gyre speed (Kwok et al., 2016, 2017).

# METHODS

## Study area and species

This study focused on two Adélie penguin (hereafter ADPE) breeding colonies at the southernmost extent of their breeding range on Ross Island in the southwestern Ross Sea (Figure 1) at Cape Crozier (169°14′ E, 77°27′ S), one of the largest known colonies in the world with ~300,000 breeding pairs, and Cape Royds (166°10′ E, 77°33′ S) with ~2500 breeding pairs. Adults at these colonies spend up to 9 months of their annual cycle north of their breeding grounds, within and north of the Ross Sea.

## Geolocator deployment

Geolocating dive recorders (22 × 21 × 15 mm, weight = 4 g, from Atesys, Strasbourg, France, hereafter referred to as

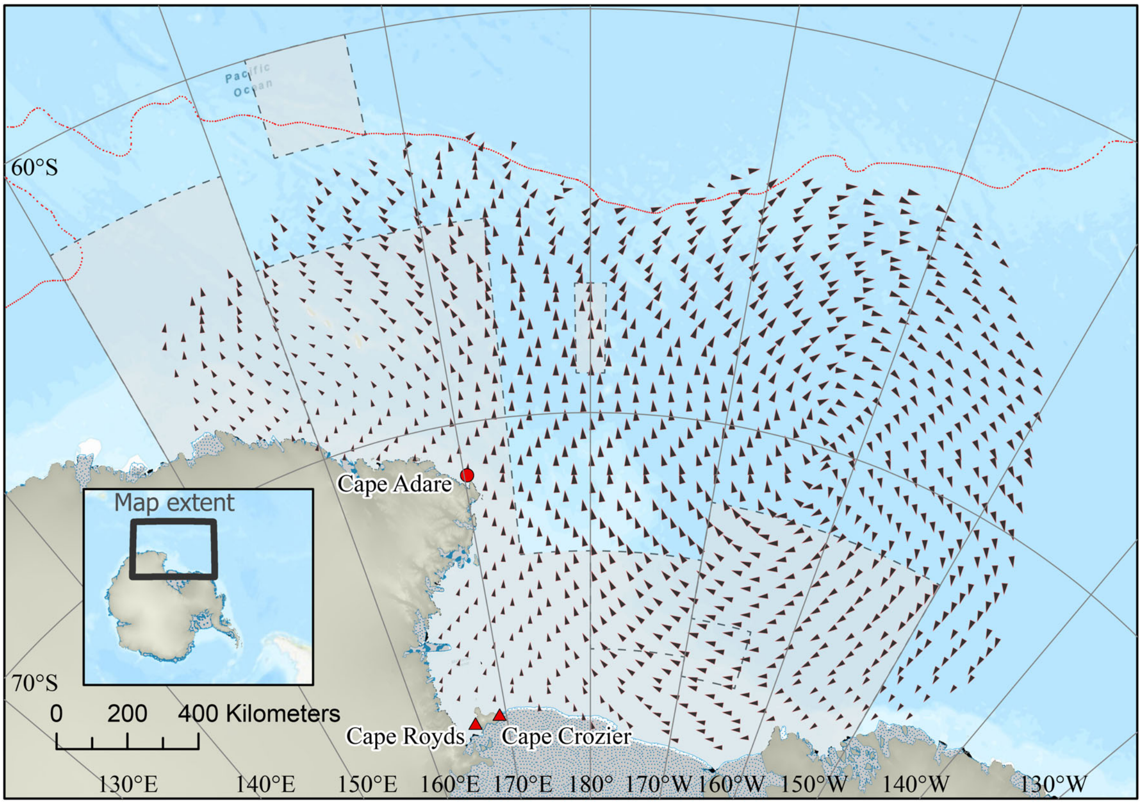

**FIGURE 1** Example sea-ice vectors for August 2019 (Tschudi et al., 2019) are shown as black arrows indicating ice direction and with larger size indicating higher relative speeds. Study colonies are indicated with red triangles. Cape Adare is indicated with a red circle for reference. The inset map indicates the extent boundary of the larger map. Boundaries of the Ross Sea Region Marine Protected Area are within dashed gray lines and shading. The average southern boundary of the Antarctic Circumpolar Current is shown as a red line (Park & Durand, 2019). The Antarctic coastline (Gerrish et al., 2022) and latitude and longitude (light gray lines) are shown for reference. Map projection is WGS 1984 Antarctic Polar Stereographic EPSG 3031.

GDRs) were deployed on known-age penguins (i.e., birds flipper-banded as chicks) during three consecutive breeding seasons (2016–2018) and left on for an entire year. Data from the recovered GDRs are referred to by the year they were recovered (e.g., GDRs deployed in November 2018 and recovered in November 2019 referred to as 2019). Individuals were selected from the pool of known-age breeding penguins, while striving to attain a balanced representation of age and sex. The GDRs measured light level every 60 s, temperature every 30 s, and pressure every second. Sensors were enclosed in a transparent flexible plastic strap and attached to the tibiotarsus above the tarsus joint using a 4 mm-wide polyester-coated stainless-steel cable tie to secure the ends of the strap together. The leg band was custom fitted to each individual so that it could spin freely on the leg, but not slip over the joint. Penguins were equipped during incubation which allowed us to monitor the state of the equipped leg. In a few cases during the first year when methods were being developed, some penguins exhibited signs of discomfort shortly after deployment. These individuals were recaptured, and the device was adjusted or removed. Most deployments were completed in 5–10 min from capture to release. If a penguin returned to the colony the following year, it was recaptured, the existing tag removed, and a new tag deployed. After deployment, nests were monitored to determine breeding success.

## Geolocation estimation

All calculations were performed in R v.4.0.5 (R Core Team, 2021). Two penguin geographic locations per day were determined from light data using a light level threshold method (set to 1 log lux) to estimate sunrise and sunset times (Lisovski et al., 2020). For each tag, light values were plotted and twilight events were annotated using the R package *TwGeos* (Lisovski et al., 2016).

After calibration using twilight events for periods at a known site and correction of clock drift, an initial path of locations was estimated for each penguin using the *SGAT* package (Lisovski & Hahn, 2012; Sumner et al., 2009). The utilized model estimates locations from twilight detections ($x$-locations) and midpoint positions ($z$-locations). In our analysis, we used the midpoint locations, resulting in a time difference of 12 h (±half of the twilight error) between successive location estimations. This approach mitigates for changes in day length throughout the year and for potential sinusoidal/tacking movement effects between consecutive twilights. Initial path estimates were then refined within a Bayesian framework using Markov chain Monte Carlo (MCMC) simulations informed by the twilight events, their error distribution, information on the last and first date at the colony, and a movement model. Our study employed the median locations from the MCMC iterations (representing the most probable track) and the 95th% around the median as a credibility interval derived from the last 500 of 2000 iterations of the MCMC simulations. In our linear mixed-effects regression models (outlined below) we used the distance from the median locations to the locations of the credibility interval as weights to account for the uncertainty in estimates. See Appendix S1 for further details on location estimate procedures.

## Penguin movements

We truncated all locations to include only those occurring between 1 April and 31 October each year due to light level constraints when periods of 24 h of daylight did not allow us to obtain positions. Some tracks did not contain data across all months due to tag failure (11 out of 146 tracks). These incomplete tracks were included in model analyses, but only complete tracks were used when summarizing total distances traveled (see below). Penguin track distance (in meters), speed (in meters per second), and bearing (in degrees) were calculated using the *geosphere* package (Hijmans et al., 2019) for each successive pair of locations along a penguin trajectory.

Visual assessment of all individual penguin tracks showed two broad migration patterns: a western route characterized by birds moving toward and west of Cape Adare and an eastern route characterized by birds moving north but largely staying east of 180° (Figures 1 and 2). Tracks with mean longitude values west of 180° were classified as “western” and those east of 180° were classified as “eastern.”

To understand how eastern and western routes differed in penguin speed and arrival date, we assessed the average speed of penguins (in meters per second) as well as arrival dates (Julian day where 0 is January 1st) as explained by migration route within a set of linear models. For arrival dates, the breeding colony was also included as an explanatory variable.

## Sea-ice data

Raster processing was performed using the *raster* package v.3.4-5 (Hijmans, 2020). Sea-ice concentration (percent area covered with sea ice) was derived from the Advanced Microwave Scanning Radiometer sensor aboard the GCOM-W1 satellite using an algorithm described in Spreen et al. (2017) and downloaded as daily 6.25 km grids from the University of Bremen (https://seaice.uni-bremen.de/start/data-archive).

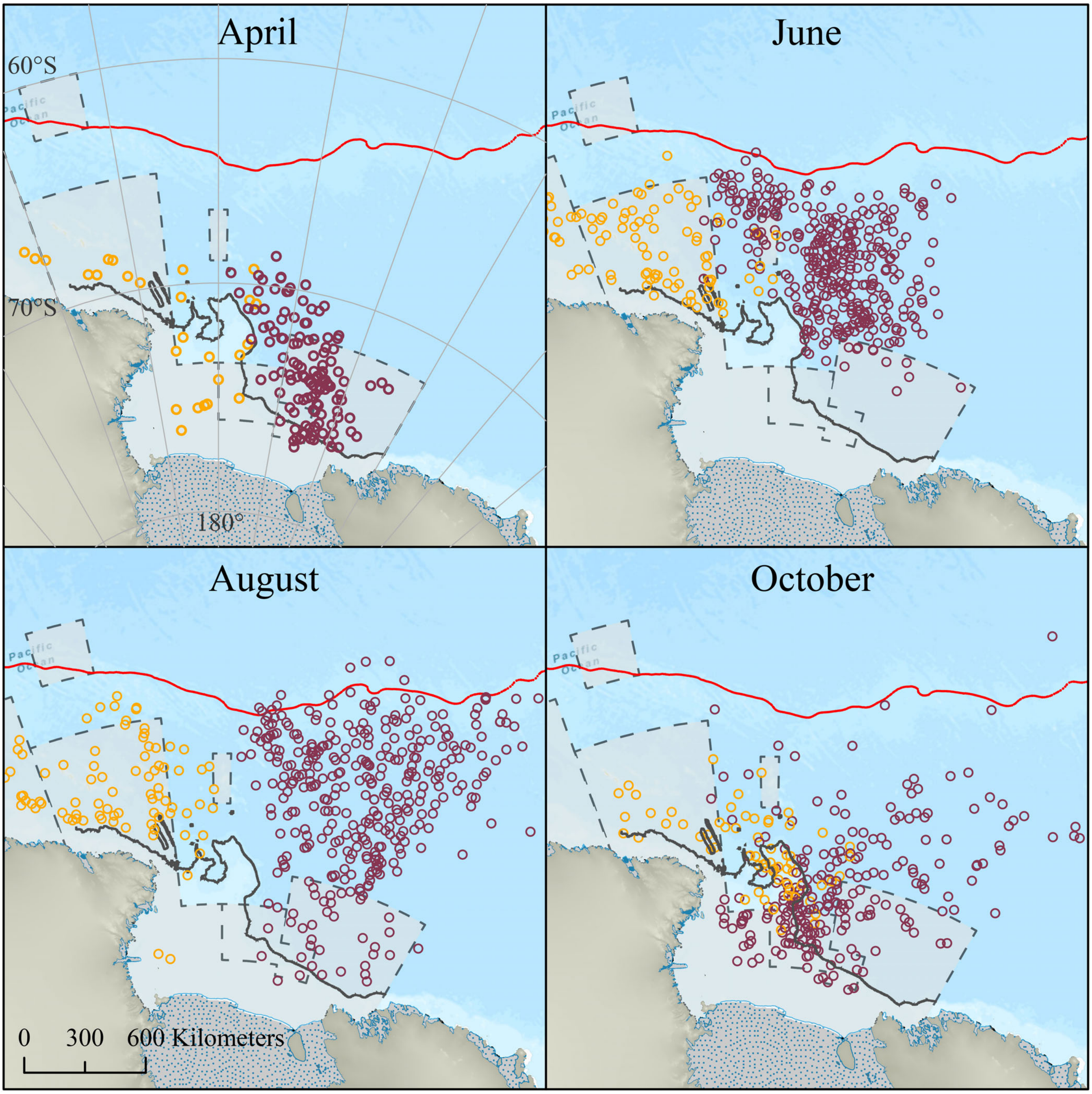

**FIGURE 2** Penguin locations for April, June, August, and October of 2019 as examples of broad movement patterns within a year and between western (orange circles) and eastern (red circles) migrating birds. The Ross Sea shelf break (200-m isobath) is shown as a solid gray line (Davey, 2013). Boundaries of the Ross Sea Region Marine Protected Area are within dashed gray lines and shading. The average southern boundary of the Antarctic Circumpolar Current is shown as a red line. The Antarctic coastline is shown for reference.

Ice velocity in centimeters per second was obtained from the Polar Pathfinder data set (version 4), which consists of daily 25 km grids of sea-ice motion vectors available via the National Snow and Ice Data Center (Tschudi et al., 2019). We applied a rotation matrix to the along-$x$ ($u$) and along-$y$ ($v$) components of the ice motion data to convert them to directional components (i.e., east and north) needed for our calculations where $L$ is the longitude:

$$u_{\text{east}} = u \times \cos L - v \times \sin L \tag{1}$$

$$v_{\text{north}} = u \times \sin L + v \times \cos L \tag{2}$$

## Calculation of ice support and drift angle

To evaluate the relationship between penguin movement and ice flow, we calculated a set of vectors (Table 1).

**TABLE 1** Definitions of (a) dependent and (b) independent variables in our models and of the (c) vectors used to define movement metrics.

| Name | Definition |
|---|---|
| (a) Dependent variables | |
| Dist5day | Total distance traveled in meters over 5 days |
| Support5day | Ice support metric (projection of Vi onto Vp) averaged across 5 days. |
| Mean latitude | Penguin mean monthly latitude in decimal degrees by migration route and year. |
| (b) Independent Variables | |
| Drift5day | Difference in angle in degrees between Vp and Vt averaged across 5 days. |
| Divesum5 | Total time spent diving in hours summed across 5 days. |
| Year week | Week number within a given year. |
| Year | Year of study as a factor. |
| Migration | Migration route classified as “east” or “west” using average location west or east of 180° longitude. |
| Sex | Sex of individual as factor (male or female). |
| Age | Age of individual in years. |
| Breeding.F | Classification of nonbreeder (0), failed (1), or successful breeder (2) as a factor. |
| (c) Vectors | |
| Vt | Penguin track speed and direction vector |
| Vi | Ice speed and direction vector |
| Vp | Penguin speed and direction vector relative to ice movement (Vp + Vi = Vt) |
| Vs | Ice support metric (projection of Vi onto Vp) quantifying the synchrony between penguin and sea ice movement vectors |
| δ | Difference in angle between Vp and Vt |

Sea-ice motion $u$ and $v$ components were used to calculate ice speed and ice bearing for each estimated penguin location:

$$\text{Ice speed} = \sqrt{\left(u_{\text{east}}^2 + v_{\text{north}}^2\right)} \times 0.01 \tag{3}$$

$$\text{Ice bearing} = 180 \times \left(\frac{a\tan 2(u_{\text{east}}, v_{\text{north}})}{\pi}\right) \tag{4}$$

With the calculated speed and direction of the penguin we calculated the relative movement to the ice flow ($\overrightarrow{Vp}$) where θ is the angle between the bearing of the ice flow and the penguin movement.

$$\overrightarrow{Vp} = \sqrt{\begin{array}{l}\text{track speed}^2 + \text{ice speed}^2 - 2 \times \text{track speed} \\ \times \text{ice speed} \times (\cos\,(\theta \times \pi/180))\end{array}} \tag{5}$$

Ice support ($\overrightarrow{Vs}$), was calculated assuming that penguins adjust their bearing in response to the underlying ice flow to reach an intended destination (i.e., full compensation; Safi et al., 2013). Based on this theory the component of ice support in the penguin's movement can be calculated using the following equation:

$$\overrightarrow{Vs} = \frac{u_p \times (u_{\text{east}} \times 0.01) + v_p \times (v_{\text{north}} \times 0.01)}{\sqrt{u_p^2 + v_p^2}} \tag{6}$$

Positive $\overrightarrow{Vs}$ values indicated that the penguin movement was supported by the ice flow. Ice support can range between 100% when the direction and speed of the penguin match the speed and bearing of the ice flow (e.g., penguin is not actively moving but drifting with the ice), to 0% or even negative values if the penguin moves against the ice flow (Appendix S2: Figure S1). For example, no penguin movement (based on geolocation estimates) but underlying ice flow results in negative support given that the penguin did move against the flow to maintain its location (Tarroux et al., 2016).

Drift was calculated as the angle difference between $\overrightarrow{Vt}$ and $\overrightarrow{Vp}$ (Table 1). Both vectors were calculated for each time step. To account for uncertainty in location estimates and temporal autocorrelations, ice support and drift values were averaged within 5-day periods for each individual.

## Calculation of the northernmost penguin latitude and strength of the Ross Gyre

To calculate penguin latitude in relation to the velocity of the Ross Gyre, we first filtered out the 25% least likely penguin locations as determined by the distance to the 95th% credibility interval. These occurred near the equinoxes and fell between 1 April and 19 April, and between 17 August and 26 September each year. We then retained the northernmost latitude for each individual track each year, which occurred either in July or August.

We used the gridded ice speed (in meters per second) from April through August as an index of the strength the Ross Gyre penguins would encounter as they travel north within each migration sector (east or west of 180°; see Appendix S1 for more details on how these sectors were defined). Within these sectors we calculated mean ice speeds across all grid cells for each year of the study.

## Distance and ice support linear mixed-effect models

To test our first prediction that penguins would travel longer distances when their speed and direction aligned with those of sea ice, the total distance (in meters) between successive locations over a 5-day period was used as the dependent variable with ice support and drift angle as the primary independent explanatory variables of interest within a linear mixed-effects "distance" model. We also assessed the additive effects of sea-ice concentration, week, year, and an interaction between week and year as well as the effect of the interactions between migration route and ice support and drift angle. We applied a log transformation to the dependent variable to meet assumptions of homogeneity of variance in the residuals. Coefficients for this model are in reference to this log-transformed space but for ease of interpretation our model plots are in the back-transformed space.

To test our second prediction that favorable ice movements would occur when penguins are traveling north away from their breeding colony or south returning to their breeding colony, ice support was used as the dependent variable with a quadratic term of week as the primary explanatory variable of interest within a linear mixed-effects "support" model. We assessed an interaction between week and migration route to account for different ice conditions between the two regions.

To account for potential differences in movement and foraging patterns by sex, age, and breeding status (Ballard et al., 2001; Lescroël et al., 2019, 2020), we assessed these individual characteristics in both models described above. Additionally, we assessed the effect of total time spent diving over each 5-day period because this could affect the total distance a penguin travels. Pressure data were used to derive dive statistics and classification using several processes modified from the *diveMove* package v1.4.5 (Luque, 2007) according to the methods detailed in Lescroël et al. (2021). Briefly, to identify dives and compute the total time spent diving we calculated dive duration, maximum dive depth, bottom time, and the number of changes in amplitude between ascent and descent. Dives were classified as "exploratory," "foraging," and "other" and the total time across all dive types was summed. Birds were sexed via DNA extracted from feather samples or by a combination of behavior, body and bill size, and timing of colony attendance (Kerry et al., 1992). Annual breeding status was classified as nonbreeding (never seen with a chick or egg that breeding season), failed (seen with an egg or chick but did not raise to crèche, the last stage of chick rearing before fledging), or successful (at least one chick raised to crèche) before the start of migration. To examine correlations between covariates we calculated Pearson correlation coefficients using the *corrplot* package (Wei & Simko, 2021) in R (Appendix S2: Figure S2).

Starting with a full fixed-effect structure, we developed models with and without a random intercept for individual penguins using linear mixed-effects models fitted with the *nlme* package (Pinheiro et al., 2021) in R. Models were fitted using restricted maximum likelihood (REML) estimation (Zuur et al., 2009) and we used the Akaike Information Criterion (AIC) to select the best random effect structure. We then used the best random effect structure and evaluated all possible subsets of the full fixed-effect structure using AIC. Models at this stage were fitted using maximum likelihood estimation (ML). Only models within two AIC of the top model were considered in our results and the top model was refitted using REML estimation (Zuur et al., 2009). We determined the strength of evidence supporting specific effects by examining the unstandardized effect sizes and the associated 95% confidence intervals (CIs). If the 95% CI for a coefficient in a competitive model ($\Delta AIC < 2.0$) included zero, it was considered uninformative (Arnold, 2010). Means ± SE are presented unless indicated otherwise. To assess model fit we used the marginal $R^2$ (Nakagawa & Schielzeth, 2013) from the *R performance* package (Lüdecke et al., 2021) as a measure of goodness-of-fit for mixed-effects models.

## Gyre strength model

To test our third prediction that higher velocity of the Ross Gyre would result in the penguins being advected farther north, we tested for the differences in northernmost latitudes reached by individual penguins between years of different gyre velocity, within each migration sector. We used mixed model analyses of variance with the *nlme* and *car* packages (Fox & Weisberg, 2019) with the northernmost latitude as the dependent variable, year as a fixed independent factor and bird ID as a random intercept. When significant differences were found, we then performed a Tukey post hoc analysis using the package *lsmeans* (Lenth, 2016) to identify which year mean differed from the others. We also tested for differences in mean ice speed between migration sectors using a Wilcoxon rank sum test.

# RESULTS

We analyzed a total of 5611 locations across 146 trips for 87 total individuals of known age. Of these, 30 trips were classified as western, and 116 trips were classified as eastern. Of the 47 trips by Cape Royds birds, 27 (57.4%) were classified as eastern. Of the 99 trips by Cape Crozier birds, 89 (89.9%) were classified as eastern trips.

On average, penguins with complete tracks (178 total, including birds of unknown age) traveled 11,318 km (median 11,159 km; SD 1708 km; Table 2) spanning April through October (Appendix S2: Table S1). The average speed of western birds was 0.71 m/s (SE = 0.008, $n = 1222$) while that of eastern birds was 0.76 m/s (SE = 0.004, $n = 4488$). Eastern birds moved about 6% faster than western birds ($\beta = 0.044 \pm 0.009$; $t\,(5706) = 4.86$, $p < 0.001$). After winter migration, western birds tended to arrive at their breeding colony about 3 days later than eastern birds, but the difference was not statistically significant ($\beta = 3.24 \pm 1.9$; $t\,(117) = 1.67$, $p = 0.09$). There was no significant difference found in arrival dates between the two different colonies during the years of our study (Cape Royds $\beta = 2.08 \pm 1.7$; $t\,(117) = 1.22$, $p = 0.22$).

## Distance model

The distance model with random effects had far more support than the model without random effects ($\Delta$AIC = 100.22). Assessing fixed effects, the top model included effects of ice support, drift, the interaction between week and year, time spent diving, breeding status, sex, and migration route (Table 3; marginal $R^2 = 0.87$). There were five other competitive models with $\Delta$AIC <2. These models all included the same terms as the top model with the addition of either (1) age, (2) an interaction between migration route and support, (3) both age and the interaction between migration route and support (4) an interaction between migration

**TABLE 2** Summary of total distances traveled in kilometers across all birds and by migration route.

| Migration | Mean | Median | Standard deviation | Maximum | Minimum |
|---|---|---|---|---|---|
| All | 11,318.59 | 11,159.76 | 1708.06 | 18,634.45 | 6791.16 |
| West | 11,001.52 | 10,825.16 | 1965.42 | 16,051.39 | 6791.16 |
| East | 11,396.20 | 11,173.47 | 1637.32 | 18,634.45 | 7937.83 |

*Note*: Values were calculated from summing daily distances traveled between every location for individual penguins with complete tracks from April through October. Distances between western and eastern migration routes were not significantly different.

**TABLE 3** Distance model subset for those within two AIC of the top model.

| Model object | Model | −2LogLik | AIC | ΔAIC | Lik | AIC weight | Marginal $R^2$ |
|---|---|---|---|---|---|---|---|
| Distmod1 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year.f + sex | 4160.24 | 4192.24 | 0 | 1 | 0.30 | 0.87 |
| Distmod2 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year + sex + age | 4158.41 | 4192.40 | 0.164 | 0.92 | 0.28 | 0.87 |
| Distmod3 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year.f + sex + support5day:migration | 4159.65 | 4193.65 | 1.413 | 0.49 | 0.15 | 0.87 |
| Distmod4 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year + sex + support5day:migration + age | 4157.84 | 4193.84 | 1.601 | 0.45 | 0.14 | 0.87 |
| Distmod5 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year + sex + drift5day:migration | 4159.96 | 4193.96 | 1.72 | 0.42 | 0.13 | 0.87 |
| Distmod6 | Breeding.f + drift5day + migration + sic5day + divesum5 + support5day + year + yearweek + yearweek:year.f + sex + drift5day:migration + age | 4158.11 | 4194.11 | 1.869 | 0.39 | 0.12 | 0.87 |

route and drift, and (5) age and the interaction between migration route and drift. All terms shared across the top and competitive models were informative (i.e., 95% CIs did not include zero) and had the same coefficient direction among each variable, but additional terms that occurred only in competitive models were uninformative.

Within the top model, ice support had a significant and positive effect on distance traveled (β = 0.96 ± 0.09, 95% CI = 0.78 to 1.13; Appendix S2: Table S2). An increase of ice support from 0.0 to 0.2 translated to ~50 additional kilometers traveled over 5 days (Figure 3a). Drift angle had a significant negative effect on distance traveled (β = −0.026 ± 0.001, 95% CI = −0.027 to −0.025) where an increase in drift angle from 20 to 30° translated to a decrease of 45 km traveled over 5 days (Figure 3b). For the interaction term between year and week, in 2018 (β = −0.009 ± 0.001, 95% CI = −0.01 to −0.007) and 2019 (β = −0.001 ± 0.001, 95% CI = −0.01 to −0.008), birds traveled a significantly shorter total distance as the season progressed compared to 2017 (Figure 3c). The amount of time spent diving (β = 0.005 ± 0.001, 95% CI = 0.004 to 0.006) had a significant positive effect with approximately each additional hour spent diving resulting in an additional kilometer traveled over 5 days (Figure 3d). Sea-ice concentration was negatively correlated with distance traveled (β = −0.002 ± 0.0005, 95% CI = −0.003 to −0.0006), with 10 km less distance covered over 5 days between locations found in 100% versus 75% sea-ice concentration (Appendix S2: Figure S3).

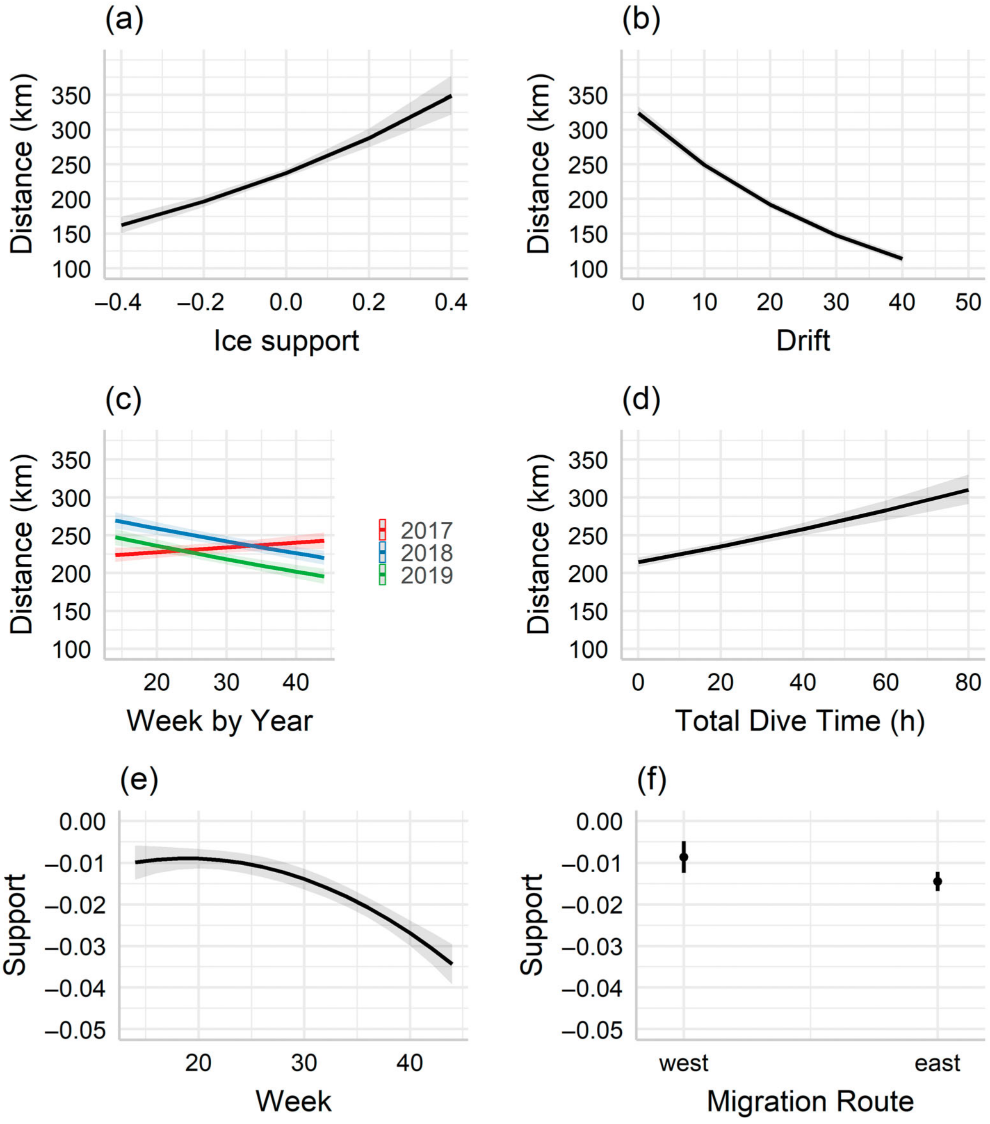

**FIGURE 3** Plots of top linear mixed-effects model of distance by ice support (a), drift (b), week by year (c), and total dive time (d). Model predictions are back transformed from log space for plotting using the *R ggeffects* package (Lüdecke, 2018). Model marginal $R^2 = 0.86$. Predictions of top linear mixed-effects model of ice support by week (e) and migration route (f). Model marginal $R^2 = 0.71$.

Penguins in the eastern sector traveled significantly longer distances than those in the western sector ($\beta = 0.13 \pm 0.02$, 95% CI = 0.10 to 0.17), moving approximately 31 km further over a 5-day period. Successful breeders also traveled significantly longer distances than nonbreeders ($\beta = 0.07 \pm 0.02$, 95% CI = 0.03 to 0.10), moving approximately 15 km further over 5 days. There was no significant difference found between nonbreeders and failed breeders ($\beta = 0.03 \pm 0.02$, 95% CI = −0.01 to 0.06). Males traveled significantly shorter distances than females ($\beta = -0.06 \pm 0.02$, 95% CI = −0.10 to −0.02), moving ~13 km less distance for each 5-day period. The interaction between ice support or drift with the migration route was not supported by our models.

## Support model

Random effects were strongly supported relative to the model without a random intercept for individual penguins (ΔAIC = 737.35), so we proceeded to model fixed effects using the random effects model. Assessing fixed effects, the top model included year, the quadratic effect of the week, and the linear effect of the migration route (Table 4; marginal $R^2 = 0.71$). There were three other competitive models within two AICs of the top model. These included the same terms as the top model, with the addition of either (1) breeding status, (2) total dive time, or (3) age. However, additional terms beyond those in the top model were uninformative.

Based on the top model we found that ice support started off higher, increasing slightly in April and May when birds were moving northward, but then decreased steadily for the rest of the winter ($\beta1 = 0.45 \pm 0.05$, 95% CI = −0.56 to −0.35; $\beta^2 = -0.19 \pm 0.05$, CI = −0.29 to −0.09; Figure 3e). Ice support was lower for eastern birds than western birds ($\beta = -0.006 \pm 0.002$, 95% CI = −0.01 to −0.002; Figure 3f). Ice support in 2018 ($\beta = 0.007 \pm 0.002$, 95% CI = 0.003 to 0.01) was higher than in 2017 and 2019 ($\beta = 0.002 \pm 0.002$, 95% CI = −0.001 to 0.006; Appendix S2: Table S3).

## Gyre strength linear model

The northernmost latitude reached by western-migrating birds did not vary by year ($\chi^2_{2,39} = 0.65$, $p = 0.72$, Figure 4) and birds in the western sector experienced significantly lower ice speeds (range 0.086–0.102 $\text{m s}^{-1}$) than eastern-migrating birds (range 0.128–0.146 $\text{m s}^{-1}$, Wilcoxon test: $W = 0$, $p < 0.001$). Conversely, the northernmost latitudes of eastern-migrating birds differed between years ($\chi^2_{2,154} = 42.13$, $p < 0.001$) as birds were found significantly further north in 2018 ($\beta = -65.2 \pm 0.274$, 95% CI = −65.7 to −64.6) and 2019 ($\beta = -65.7 \pm 0.316$, 95% CI = −66.3 to −65.00), when ice speeds were higher, compared to 2017 ($\beta = -67.4 \pm 0.291$, 95% CI = −68.0 to −66.8, different from 2018 and 2019 at $p < 0.001$). Hence, eastern-migrating birds were found ~244 km farther north in 2018, when ice speed was the highest, compared with 2017.

# DISCUSSION

We present evidence confirming that winter movements of ADPE are in part shaped and influenced by the movement of sea ice. Our results corroborate and expand upon previous studies (Ballard et al., 2010; J. Clarke et al., 2003; Takahashi et al., 2018; Thiebot et al., 2019) by integrating both speed and direction at 5-day intervals to show that birds achieved longer distances when they received support from the movement of ice. Furthermore, our results also show that penguins can be impeded by sea-ice movement, with higher drift angles associated with slower traveling speeds (shorter distances traveled over 5-day intervals). Finally, on the eastern (primary) migration route, penguins were associated with lower latitudes (i.e., more north) as the strength of the Ross Gyre increased, further indicating a need to balance the benefits and costs of riding on ice floes.

The propulsion method and body size of a species in interaction with the medium through which they travel influence the strategies, constraints, and opportunities

**TABLE 4** Support model subset within two AIC of the top model.

| Model object | Model | −2LogLik | AIC | ΔAIC | Lik | AIC weight | Marginal $R^2$ |
|---|---|---|---|---|---|---|---|
| Supmod1 | Poly (year week, 2) + migration + year | −17,175.58 | −17,159.64 | 0 | 1 | 0.39 | 0.73 |
| Supmod2 | Poly (year week, 2) + migration + year + Breeding.f | −17,179.09 | −17,159.14 | 0.5 | 0.78 | 0.31 | 0.73 |
| Supmod3 | Poly (year week, 2) + migration + year + divesum5 | −17,175.80 | −17,157.84 | 1.8 | 0.41 | 0.16 | 0.74 |
| Supmod4 | Poly (year week, 2) + migration + year + age | −17,175.59 | −17,157.65 | 2 | 0.37 | 0.14 | 0.73 |

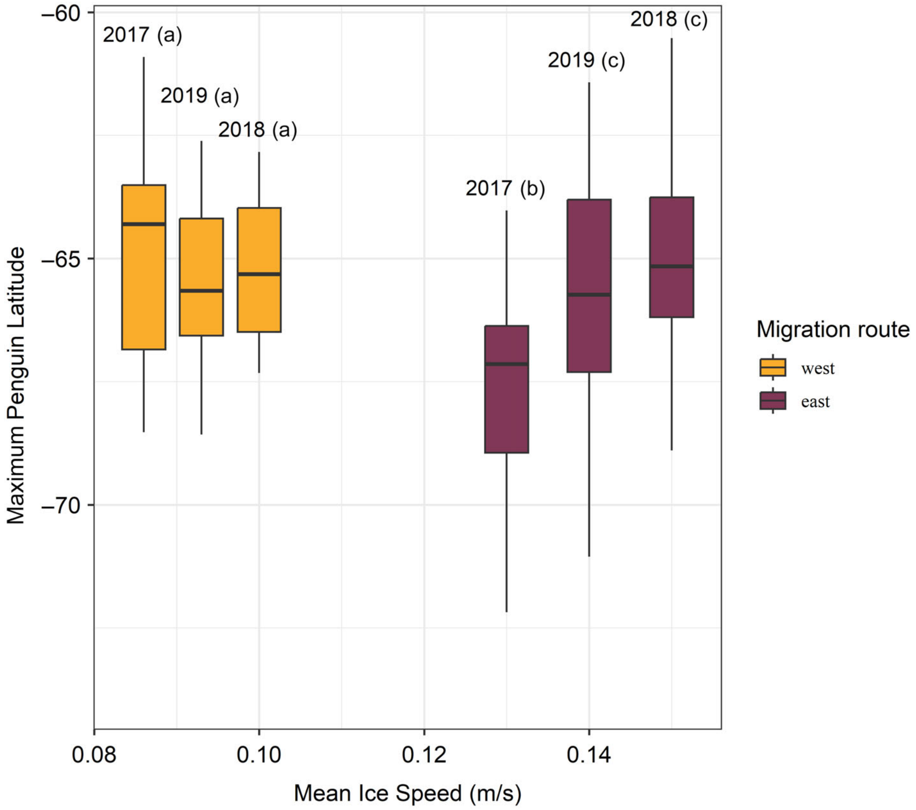

**FIGURE 4** Boxplot of maximum penguin latitudes against Ross Gyre speeds by year and migration sector (west or east). Within each migration sector, boxes sharing the same letter (a, b or c) are not statistically different from each other.

available to them (Chapman et al., 2011). In comparison with other species that walk or swim, the maximum distances our study species traveled exceeded those found for other species of similar size (Hays & Scott, 2013). The ability to travel these long distances may be facilitated by the ice support that we documented in our investigation. Alternatively, wildlife might exceed anticipated distances by feeding en route or through reduced temporal pressures to complete their movements (Alerstam et al., 2003; Hays & Scott, 2013). However, for our study species, foraging dives were at their lowest as they moved north (Lescroël et al., 2023) and breeding ADPE must also make these migrations on an annual basis within a specific timeframe defined by the highly seasonal constraints of Southern Ocean daylight and prey availability.

Our results indicate that ADPE may be adjusting to large differences in the direction and speed of sea ice depending on the phase of their migration. As predicted, overall ice support was higher when penguins were moving north in April and May. However, they did not receive the predicted support on their return/southward prebreeding movements. Temporal variability in the cyclonic pattern of the Ross Gyre may partially explain this decreased support as the clockwise movement in ice drift patterns that we predicted penguins would use to facilitate their movement south begins to weaken in July–August (Kwok et al., 2017). Thus, our study species would be traveling against the predominantly northward and/or eastward moving ice drift as they head back to the colony in September through October. It is not uncommon for species to experience differences in the direction of flow depending on the phase of their migration (Chapman et al., 2011). As an adaptation, some species may compensate by adjusting their height in air or depth in water to find more favorable currents (Metcalfe et al., 1990; Tarroux et al., 2016) but this response is not available to species that walk on sea ice. Alternatively, when movement support is not possible or used, species may prioritize refueling, depending on their energetic needs and food availability (Amélineau et al., 2021; Sleeman et al., 2010). For example, Arctic terns have been found to rely more on wind support to travel north but prioritize locating high-productivity areas to refuel during southward movements when facing more headwinds (Hromádková et al., 2020). Our study species may employ a similar strategy, with increased diving/foraging activity ramping up in July and increasing throughout their return to the breeding colony, also coinciding with the need to build energy reserves for fasting during territory establishment, laying and incubation (Lescroël et al., 2023).

Overall, our results broadly align with those found for other migrating (flying) seabirds where breeding colony size, competition, individual characteristics, and local habitat conditions all play a role in shaping migratory routes and behaviors (Campioni et al., 2020; Fayet et al., 2017). Here we found that the distances individuals covered, as well as the amount of ice support they received, were related to the migration route they took as well as individual characteristics (i.e., sex and breeding status). While most birds breeding at the large Cape Crozier colony took an eastern route, about half of the birds from the small Cape Royds colony did so. Our distance model indicated that eastern birds moved approximately 6 km/day further than western birds, but our support model indicated that they received less ice support overall. Taken together this may mean that eastern birds were expending more energy to migrate. This could come at a cost or may be compensated through other benefits (Dufour et al., 2021) such as accessing higher prey concentrations by avoiding high levels of intraspecific competition along the northern Victoria Land coast, where several other large ADPE colonies have been increasing over the last ~20 years (Lynch & LaRue, 2014). Females, successful breeders, and more time spent diving were also correlated with traveling longer distances. However, within our support model, we did not find evidence indicating that any of these characteristics explained the variation in the amount of ice support received. Female ADPE exhibit extended travel distances and times during breeding season foraging bouts (J. Clarke et al., 1998; Lescroël et al., 2010) and perform more foraging dives per hour throughout the annual cycle (Lescroël et al., 2023). The correlation between dive frequency and travel distances in ADPE (Ford et al., 2015) suggests sex differences in distance traveled and foraging intensity over the winter could be explained by differences in energetic requirements such as egg formation in females, which is initiated before reaching the breeding grounds (Astheimer & Grau, 1985), or carryover effect from the breeding season. Successful breeders, having to provide for their chicks over a longer period and exhibiting the highest rate of foraging dives during rearing (Lescroël et al., 2023), may also need to replenish their energetic stores at a higher rate than non or failed breeders, possibly influencing migratory strategies. Our results therefore highlight the complex interplay between biotic, abiotic, individual, and population factors that shape migratory behaviors and call for a critical examination of migration patterns across a larger set of colonies and conditions to further understand what drives migratory strategies at a regional scale (Fayet et al., 2017).

Sea ice, a distinctive medium compared with air or fluid substrates, exerts unique effects on species engaged in long-distance movements. Its attributes, encompassing seasonality, thickness, concentration, and freeze/melt dynamics, exhibit a regional specificity surpassing that of wind or ocean currents (Stammerjohn, Martinson, Smith, & Iannuzzi, 2008; Worby et al., 2011). Sea ice can simultaneously serve as a traversable pathway, shelter (from weather and predation), and habitat for prey species. These varied roles introduce intricacies into the impact of changes to sea ice and may lead to higher variability in behavioral responses and interactions than other fluid mediums. For example, studies of polar bear (*Ursus maritimus*) movement, another sea ice obligate species, show that regional disparities in ice attributes can influence energetic budgets and timing of seasonal movements (Klappstein et al., 2020; Mauritzen et al., 2003). Polar bears, who rely on sea ice for foraging opportunities, may also have to expend more energy to compensate for increases in ice drift while making decisions on when to stay on ice or return to land based on the timing of sea ice break up or melt (Cherry et al., 2013; Durner et al., 2017). In our study, western birds moving along the coast encounter thicker and more heavily deformed ice (Rack et al., 2021) associated with the dynamic wind-driven ice movement in this region. Under these circumstances, they may receive increased ice support from northward moving ice, albeit at the expense of decelerated walking speeds as they navigate over extended stretches of rough ice (Yoda et al., 2001). Ice direction and speed are therefore not the only characteristics that matter in shaping the movements and energetics of sea-ice obligate species, and, with the ongoing development of higher-resolution remote sensors and animal-borne loggers, further studies may seek to integrate other dimensions such as ice thickness, roughness, and age.

Besides the mechanistic links between penguins and sea-ice movements, our analysis has implications for the population dynamics and conservation of high-latitude Southern Ocean biota, including the southern Ross Sea ADPE population. Trends and connections between sea-ice drift, wind, ice production, and extent (Kwok et al., 2017; Parkinson, 2019; Stammerjohn, Martinson, Smith, Yuan, & Rind, 2008) over the last several decades may have consequences beyond habitat availability (e.g., Ainley et al., 2010; Ropert-Coudert et al., 2019). Increasing meridional winds producing higher ice drift may, for example, provide more ice support for penguins moving north, but may also further impede birds in their prebreeding southward movement. Because birds were found further north with higher gyre speeds, changes in ice drift may impact where they forage or how much energy they must expend to stay within favorable feeding grounds. Variation and changes in the movement of sea ice may therefore serve as a mechanism impacting annual variation in adult survival (Ballerini et al., 2009), reproductive success (Emmerson & Southwell, 2008), recruitment (Wilson et al., 2001), or breeding propensity, ultimately driving breeding population trajectories on Ross Island.

Finally, our results align with studies of other taxa that have found that ocean circulation patterns within the Ross Sea may be particularly important drivers of wildlife movement and life history. Within our study region the life history and distribution of Antarctic krill (*Euphausia superba*), crystal krill (*Euphausia crystallorophias*), and Antarctic silverfish (*Pleuragramma antarcticum*), key midtrophic level components of the food web and ADPE diet, as well as Antarctic toothfish (*Dissostichus mawsoni*), a competitor with ADPE, are shaped by oceanic currents and the Ross Gyre (Ashford et al., 2012; Brooks et al., 2018; Piñones et al., 2016). As a result, identifying functional connectivity patterns across multiple species and trophic levels and how changes to ocean currents and sea ice could impact food web dynamics and ecosystem structures remain important topics (e.g., Ashford et al., 2017). For ADPE, long-term changes in these ocean circulation patterns may influence not only their migratory routes, but the ecological interactions between predators and prey that have defined this region (Ainley et al., 2006). While several factors can influence which route is taken by migrating wildlife (e.g., Byholm et al., 2022), the movement association with sea ice we show here may limit how ADPE can respond to other changes in their environment, leading to spatiotemporal mismatches in resource availability (Robinson et al., 2009).

## ACKNOWLEDGMENTS

We are grateful for financial support provided by the National Science Foundation (OPP 1543498, 1543541, 1935870, and 1543459), NASA (80NSSC19K0189) and the National Science Foundation Graduate Research Fellowship under Grant No. 1938055 with logistic support for data collection provided by the US Antarctic Program. We thank Arvind Varsani, Jean Pennycook, Virginia Morandini, Suzanne Winquist, Parker Levinson, Emily Burke, and Katie Stoner for their tireless help out on the ice. Simeon Lisovski acknowledges funding from Geo.X, the research network for geosciences in Berlin and Brandenburg. We thank ESRI for access to GIS software via their non-profit program. All data collection protocols were approved by the Institutional Animal Care and Use Committees of Oregon State University and Point Blue Conservation Science. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. This is Point Blue Conservation Science Contribution no. 2462.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Code to calculate vector data and ice support metrics, and unmodified functions and data used to run the models, are available from Jongsomjit et al. (2023) in Zenodo at https://doi.org/10.5281/zenodo.8374474.

## ETHICS STATEMENT

All penguin survey, capture and handling methods used for data collection were performed following all relevant guidelines and regulations under the approval and oversight of the Institutional Animal Care and Use Committees of Oregon State University and Point Blue Conservation Science. Additionally, all work approved and conducted under Antarctic Conservation Act permits issued by the US National Science Foundation and the US Antarctic Program.

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## SUPPORTING INFORMATION

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**How to cite this article:** Jongsomjit, Dennis, Amelie Lescroël, Annie E. Schmidt, Simeon Lisovski, David G. Ainley, Ellen Hines, Megan Elrod, Katie M. Dugger, and Grant Ballard. 2024. “Going with the Floe: Sea-Ice Movement Affects Distance and Destination during Adélie Penguin Winter Movements.” *Ecology* 105(2): e4196. https://doi.org/10.1002/ecy.4196