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ARTICLE

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The foraging behavior of nonbreeding Adélie penguins in the western Antarctic Peninsula during the breeding season

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Abstract

Information on marine predator at-sea distributions is key to understanding ecosystem and community dynamics and an important component of spatial management frameworks that aim to identify regions important for conservation. Tracking data from seabirds are widely used to define priority areas for conservation, but such data are often restricted to the breeding population. This also applies to penguins in Antarctica, where identification of important habitat for nonbreeders has received limited attention. Nonbreeding penguins are expected to have larger foraging distributions than breeding conspecifics, which may alter their interactions with physical environmental factors, conspecifics, other marine predators, and threats. We studied the movement behavior of nonbreeding Adélie penguins tracked during the 2016/2017 breeding season at King George Island in the South Shetland Islands, Antarctica. We quantify how nonbreeding penguins' horizontal moment behavior varies in relation to environmental conditions and assess the extent of spatial overlap in the foraging ranges of nonbreeders and breeders, which were tracked over several years. Nonbreeders increased their prey search and area-restricted foraging behavior as sea surface temperature and bottom depths decreased, and in response to increasing sea ice concentration. Nonbreeders tended to transit (high directional movement) over the relatively deep Central Basin of the Bransfield Strait. The majority of foraging behavior occurred within the colder, Weddell Sea–sourced water of the Antarctic Coastal Current (incubation) and in the Weddell Sea (crèche). The utilization distributions of breeders and nonbreeders overlapped in the central Bransfield Strait. Spatial segregation was greater during the crèche stage of breeding compared to incubation and brood, because chick provisioning still constrained the foraging range of breeders to a scale of a few tens of kilometers, while nonbreeders commenced with premolt foraging trips into the Weddell Sea. Our results show that breeding and nonbreeding penguins may not be impacted similarly by local environmental variability, given that their spatial and temporal scales of foraging differ during some part of the austral summer. Our study highlights the need to account for different life history stages when characterizing foraging behavior of marine predator populations. This is particularly important for "sentinel" species monitored as part of marine conservation and ecosystem-based management programs.

KEYWORDS
central-place foraging, marine predator, move persistence, nonbreeding, penguin, *Pygoscelis adeliae*, seabird, tracking data, utilization distribution

INTRODUCTION

Marine predators play a critical role in the structure, functioning, and resilience of marine ecosystems (Baum & Worm, 2009). Key to understanding these ecological roles is resolving the spatiotemporal patterns in marine predator distribution and abundance (Hays et al., 2016). Satellite monitoring of marine predators can reveal information about the movement decisions of individuals and populations, which, in turn, can provide insight into fundamental ecosystem processes (Ropert-Coudert et al., 2020). For example, tagging and tracking of marine predators can identify areas of ecological significance to predators, which may be indicative of broader ecosystem structuring, such as areas of high biodiversity and biomass at lower trophic levels (Hindell et al., 2020). However, most tracking studies of marine predators focus on breeding adults, with much less known about the movement behavior of juveniles and nonbreeders (Hays et al., 2016).

Substantial reductions in global marine predator abundances, largely due to anthropogenic influences, demonstrate an urgent need for appropriate conservation and management policies (Baum & Worm, 2009). Marine predator movement data can be used to help inform spatially explicit conservation management strategies, which aim to preserve the ecological integrity of marine environments (Hays et al., 2019). However, translating tracking data into effective conservation practice remains challenging when tracking data are spatially or temporally limited, or restricted to certain life history stages. Nonbreeding seabirds, for example, are not constrained to return to land to provision offspring and may exhibit substantially different movement behaviors compared to breeders (Hinke et al., 2019; Thiebot et al., 2020). Tracking data from the breeding population alone may thus poorly represent the heterogeneous movement patterns of the total population, potentially biasing the identification of space-use hotspots and estimates of overlap with threats (Carneiro et al., 2020). In southern Africa, for example, the foraging ranges of breeding adult African penguins (*Spheniscus demersus*) were used to delineate the boundaries of a fishing exclusion marine protected area (MPA) (Ludynia et al., 2012), but this MPA fails to protect the foraging habitat of juvenile penguins, with these young birds still vulnerable to competition with fisheries (Sherley et al., 2017). Information on space use of all life history stages, and not only breeders, is therefore important for the development of spatial management and conservation strategies (Carneiro et al., 2020; Hinke et al., 2020).

Modeling at-sea distributions of marine predators is an important component of current Southern Ocean spatial management frameworks that aim to identify regions important for conservation (Hindell et al., 2020). The analysis of tracking data from Southern Ocean seabirds, and penguins in particular, has been widely used to define important areas for marine conservation in Antarctic waters. Many of these studies have focused exclusively on birds incubating or provisioning chicks, an energetically demanding period when nest duties restrict the foraging ranges of breeding adults (Dias et al., 2018; Handley et al., 2021; Warwick-Evans et al., 2018). During other life-history stages birds may have larger foraging distributions with very different spatial overlaps between conspecifics, including breeding animals from adjacent or distant colonies, other marine predators and potential threats, such as fisheries.

In this study, we characterize the at-sea distribution and habitat use of nonbreeding Adélie penguins *Pygoscelis adeliae* tracked from the South Shetland Islands during the austral summer breeding season (November–February) of 2016/2017. Adult Adélie penguins attempt to breed in most years (Hinke, Trivelpiece, & Trivelpiece, 2017), but ultimately many individuals end up as nonbreeders because they fail to pair or as a result of early nest failure (due to weather, egg predation, and other factors). Together with the younger, still reproductively maturing birds of the population, these nonbreeders comprise a significant proportion of a population (Ainley, 2002). Here, we quantify how nonbreeding Adélie penguin movement behavior varies in relation to environmental conditions encountered along tracks, and assess the extent of spatial overlap in the foraging ranges of nonbreeders and breeders, which were tracked over several years. Many Adélie penguin populations in the western Antarctic Peninsula (WAP) region have declined in recent decades in response to rapid environmental and ecosystem change (Lynch et al., 2012), with populations in the northern WAP especially vulnerable to further decline (Cimino et al., 2016; Hinke, Cossio, et al., 2017). There is also increasing concern that temporal and spatial concentration of the fishery for Antarctic krill *Euphausia superba* may affect some penguin populations in the WAP (Watters et al., 2020). While progress has been made in understanding environmental features affecting habitat selection in breeding Adélie penguins (Trathan et al., 2018; Warwick-Evans et al., 2018) and the degree of overlap between the foraging areas exploited by breeding birds and those targeted by fisheries (Hinke, Cossio, et al., 2017), there is currently no published information available on the at-sea movements of adult nonbreeding penguins (failed and skipped breeders) during the breeding season. Resolving this knowledge gap will aid our interpretations of the proximate causes of population trends and will benefit management and conservation efforts (Carneiro et al., 2020). Our first aim is to investigate how horizontal movement behavior of nonbreeding adult Adélie penguins tracked during the breeding season relates to environmental factors. Second, we assessed the extent of at-sea spatial overlap between nonbreeding and breeding Adélie penguins. We predict that nonbreeders will forage over a larger area than breeders and that segregation in space use will be greatest during the chick-rearing phases of the breeding cycle when the foraging range of breeders is most constrained by reproductive commitments.

METHODS

Nonbreeder tag deployments

Thirty location-providing Platform Terminal Transmitters (PTTs, henceforth tags; TAM-2638, Telonics, Arizona, USA) were deployed on adult nonbreeding Adélie penguins in November 2016. Tags were deployed at Adélie penguin breeding colonies located on the southern shore of King George Island (Isla 25 de Mayo), at Stranger Point (−62.27 S, −58.62 W) ($n = 15$), and at Point Thomas (within Admiralty Bay; −62.16 S, −58.46 W; $n = 15$). Penguins were captured by hand and briefly restrained to attach instruments (handling time per individual was <10 min). We used Tesa tape (4651), cyanoacrylate glue (Loctite401), and small plastic cable ties (threaded through underlying feathers and closed over the top of the tags) to attach tags to feathers along the mid-point of the back. Tags measured 64 × 28 × 18 mm and weighed 49 g, which is <1.2% of the average mass of breeding Adélie penguins (Ainley, 2002).

All tags were deployed during the incubation stage of the breeding season (6–17 November 2016) and were expected to remain attached until the penguins molted in February 2017, when tags were lost. Study colony penguins were monitored during early incubation so that tags could be deployed on individuals observed to have lost the egg(s) they were incubating (e.g., to predation by brown skua *Stercorarius antarcticus*), or on individuals occupying empty nests (e.g., because they failed to pair). The instrumented birds were then monitored daily until the end of the incubation phase to confirm that they were failed or skipped breeders (i.e., nonbreeders). Two individuals were observed to brood an egg after instrumentation; their tags were recovered and redeployed on nonbreeding individuals. We were unable to visually confirm that the instrumented birds remained nonbreeders once they departed the colony, but their movement behavior (e.g., time spent at sea) did not suggest that they bred elsewhere during the study period. We did not attempt to determine the sex of the instrumented birds.

Data processing

Tags were scheduled to transmit daily signals to the Argos CLS satellite constellation until battery failure, providing Doppler-shift estimates of location with varying accuracy (Lowther et al., 2015). Location estimates were downloaded from Argos and processed using R 3.6.3 (R Core Team, 2020). A continuous-time random walk (CT-RW) model was fitted to the raw Argos data via the R package "foieGras" (Jonsen & Patterson, 2020). The CT-RW model removed unreliable locations (we imposed a maximum travel rate of 10 km/h; Sato et al., 2010) and transformed irregular Argos location fixes to discrete predicted locations at 2-h intervals (Jonsen et al., 2020). Each resultant track was split into separate foraging trips using the R package "track2KBA" (Beal et al., 2021; Oppel, 2020). We assumed a foraging trip started when a penguin traveled 5 km or more from the breeding colony, and remained at least 6 h away from the colony. Foraging trips ended when a penguin returned to within 3 km of the colony. Distance from the colony was calculated as the great-circle distance using the function *tripSummary* of the "track2KBA" package. Defining trips this way was needed because the low-resolution Argos location data made it difficult to delineate shorter trips, even after fitting a CT-RW model (e.g., Breed et al., 2011). Locations recorded on land do not represent foraging behavior and were removed for subsequent analyses (5.7% of all locations).

To facilitate comparison with breeder foraging behavior, we assigned the foraging trips of nonbreeders to breeding stages (incubation, brood, and crèche) using the departure date of each foraging trip, and the mean transition dates between incubation, brood, and crèche periods observed from breeders (Hinke et al., 2018) (Appendix S1). In the absence of direct observations from nonbreeders (which never hatched eggs or provisioned chicks in brood or crèche), we assumed that departure dates for nonbreeder "incubation" trips ended on 30 November. Nonbreeder foraging trips with departure dates from 1 December (the mean date of hatching at Point Thomas) to 27 December were assigned to the brood stage, and trip departures from 28 December to 24 January were assigned to the crèche stage (Hinke et al., 2018). None of the tracked penguins returned to the South Shetland Islands after Adélie penguin chicks started to fledge at the end of January (Trivelpiece et al., 1987).

Habitat use of nonbreeders

We fitted move persistence mixed effects models (Jonsen et al., 2019) to the CT-RW derived at-sea locations of nonbreeders to infer relationships between their individual movement patterns and the physical environmental conditions they encountered. Unlike Hidden Markov model state-switching approaches (e.g., McClintock & Michelot, 2018) that define discrete behavioral states (e.g., "transit" and "foraging") as proxies of foraging behavior, move persistence models estimate time-varying move persistence (γ_t) along animal movement trajectories as a continuous-valued behavioral index. Move persistence (γ_t) is then the autocorrelation in both speed and direction that range from 0 (low directional persistence, or area-restricted searching) to 1 (high directional persistence, or transitory movement). To investigate which factors are associated with increasing or decreasing move persistence, we modeled γ_t as a linear function of environmental conditions encountered by penguins during their foraging trips (environmental covariates outlined below). We fitted multiple linear mixed models containing different combinations of fixed effects to assess which environmental covariate(s) best explained the movement behavior of nonbreeders. To avoid overparameterization, we did not consider more than two environmental covariates in any mixed model. Additionally, the covariates depth, distance to shelf, and distance to coast were highly collinear (Spearman rank correlation coefficients >0.7 or <-0.7) and as such were not included in the same models (Appendix S2). Random intercepts allowed a random shift of individual responses around the population intercept. Mixed models were fitted using maximum likelihood and model selection was performed using Akaike information criterion (AIC). Models with the lowest AIC values are most parsimonious and represent the best compromise between model complexity and fit (Burnham & Anderson, 2002). Relative model support was based on differences in AIC_c values (ΔAIC_c) (Burnham & Anderson, 2002). The mixed models best supported by the data were refitted using restricted maximum likelihood (REML) estimation as REML provides more reliable estimates of the variance components (Zuur et al., 2009).

Environmental covariates

Gridded bathymetry data at 500-m resolution (obtained from the General Bathymetric Chart of the Oceans [GEBCO]; https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2019/gebco_2019_info.html) were used to calculate ocean depth (in meters), distance to the shelf break (defined as the 200 m bathymetry contour) (in kilometers), and distance to the nearest coast (in kilometers) for each location in CT-RW tracks. Daily sea surface temperature (SST) data were obtained from NOAA's 1/4° daily Optimum Interpolation Sea Surface Temperature (OISST) dataset (V2.1; http://www.ncdc.noaa.gov/oisst) using the "rerddap" R package (Chamberlain, 2019). Daily sea ice concentration (%) and distance to the ice edge (defined as 15% sea ice concentration) (in kilometers) were derived from Institut Français de Recherche pour l'Exploitation de la Mer (Ifremer, ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/) sea ice data with 12.5-km spatial resolution. We used finite-size Lyapunov exponents (FSLEs) as a Lagrangian indicator of sub-mesoscale structures of ocean circulation. FSLEs are computed from satellite altimetry products and delineate surface water boundaries such as fronts, filaments, and currents (d'Ovidio et al., 2004). We used AVISO backward-in-time FSLEs at a spatial resolution of 0.04°, which are derived from SSALTO/DUACS global ocean absolute geostrophic velocities (https://www.aviso.altimetry.fr/en/data/products/value-added-products/fsle-finite-size-lyapunov-exponents.html). For analyses, we extracted environmental covariate values at every discrete location along nonbreeder penguins' CT-RW tracks and standardized the ensuing variables to mean $= 0$, SD $= 1$. We present maps of environmental covariates and all pairwise Spearman rank correlation coefficients among covariates in Appendix S2.

Comparing nonbreeder and breeder space use

The at-sea locations of Adélie penguins breeding at the Copacabana colony (within King George Island's Admiralty Bay and 1.6 km SE of Point Thomas; −62.18 S, −58.46 W) were used to describe the space use of breeding penguins (defined as individuals incubating eggs or provisioning chicks at the time of tag deployments; tracks from breeders that did not return to the breeding colony to provision chicks were not considered). Tracking data were collected between 1996 and 2013 with Argos CLS satellite tag transmitters similar to those deployed on nonbreeders (e.g., Hinke, Cossio, et al., 2017). Breeder data were thus not concurrent to that of nonbreeders but collected over a 17-year period; we assumed that the broad, population-level characterization of space use by utilization distributions (UDs) was not influenced by this temporal mismatch. We used data from deployments made during the incubation ($n = 20$), brood ($n = 13$), and crèche ($n = 33$) breeding stages to calculate breeder UDs. Raw location fixes were processed similar to that of nonbreeders (by fitting a CT-RW model), but we used field observations from tracked individuals instead of mean durations (i.e., calendar dates) of the incubation, brood, and crèche periods from phenological studies to assign each deployment to a breeding stage (Appendix S1).

Utilization distribution overlap

We quantified the extent of space use and overlap between breeders and nonbreeders at sea by calculating UDs of foraging range (95%) and core areas (50%) per breeding stage. All UD estimation and overlap analyses were conducted using the R package "adehabitatHR" (Calenge, 2006). The kernel smoothing parameter h was set to 12.5 km, which was the average area-restricted search scale for nonbreeders according to first passage time analysis performed using the "adehabitatLT" package (Calenge, 2006; Lascelles et al., 2016) (Appendix S3). We used the UD overlap index (UDOI) as a measure of the degree of overlap between foraging areas of breeders and nonbreeders. The UDOI is a modification of the Hurlbert Index of niche overlap that quantifies space-use sharing of individuals relative to uniform space usage (Fieberg & Kochanny, 2005). The UDOI values range from zero when there is no overlap of UDs, to one when there is complete overlap and uniform space use, and UDOI exceeds one when UDs have nonuniform distributions with high overlap (Fieberg & Kochanny, 2005). We used permutation analysis to test the null hypothesis that there were no segregation in the UDs of breeders and nonbreeders during each breeding stage. The null hypothesis was rejected if the overlap calculated from the observed data was significantly different from the overlap calculated from a simulated dataset (1000 permutations) in which breeding state (breeder and nonbreeder) was randomly assigned to individuals during each breeding stage. Significance (p values) was estimated as the proportion of permuted overlap scores that were smaller than the observed overlap (e.g., Botha & Pistorius, 2018; Reisinger et al., 2020). The p values calculated from Monte Carlo permutations are approximations and are thus given with 95% confidence intervals.

RESULTS

Nonbreeding Adélie penguins were tracked at sea between 10 November 2016 and 14 February 2017, with individuals providing data for 75.1 days on average (SD: 17.2 days; range: 24.8–96.2 days). Breeders (mean $=$ 134.7 km; 11.9 days) and nonbreeders (mean $=$ 124.9 km; 16.3 days) had broadly similar foraging trip distances and trip durations during the incubation stage (Table 1). During brood and crèche, nonbreeders undertook both nearby and distant foraging trips (maximum distance $=$ 851 km), whereas breeders only made nearby foraging trips (predominantly <30 km and almost always <40 km from the colony) of short duration (Figure 1, Appendix S1). All nonbreeders made multiple foraging trips (range 2–16) interspersed with returns to the breeding colony. Most nonbreeders returned to King George Island during the brood stage, often remaining there well into the crèche stage while

TABLE 1 Comparison of breeding and nonbreeding Adélie penguin tracking data collected from King George Island, South Shetland Islands, during the incubation, brood, and crèche stages of the breeding season

Breeding category	*N*	Foraging trips (*N*)	Max distance (km)	Distance (km)	df	*t*	*p*	Max duration (days)	Duration (days)	df	*t*	*p*
Incubation												
Nonbreeders	27	56	364.4	124.9 ± 63.7				63.6	16.3 ± 12.4			
Breeders	20	23	650.8	134.7 ± 103.2	29.5	0.4	0.7	26.9	11.9 ± 5.6	38.4	−1.6	0.1
Brood												
Nonbreeders	18	55	461.3	50.2 ± 69.5				28.3	6.2 ± 7.4			
Breeders	13	34	51.0	11.2 ± 5.1	17.3	2.4	0.03	2.6	1.0 ± 0.5	17.2	−2.9	<0.01
Crèche												
Nonbreeders	27	90	852.2	212.0 ± 115.7				39.7	11.6 ± 11.1			
Breeders	33	90	95.2	14.5 ± 9.4	26.3	8.8	0.01	4.2	1.1 ± 0.8	26.2	−4.9	<0.01

Note: Welch *t* tests were used to compare the mean distance from the colony and mean duration of foraging trips. Distance and duration values are given as mean ± SD.

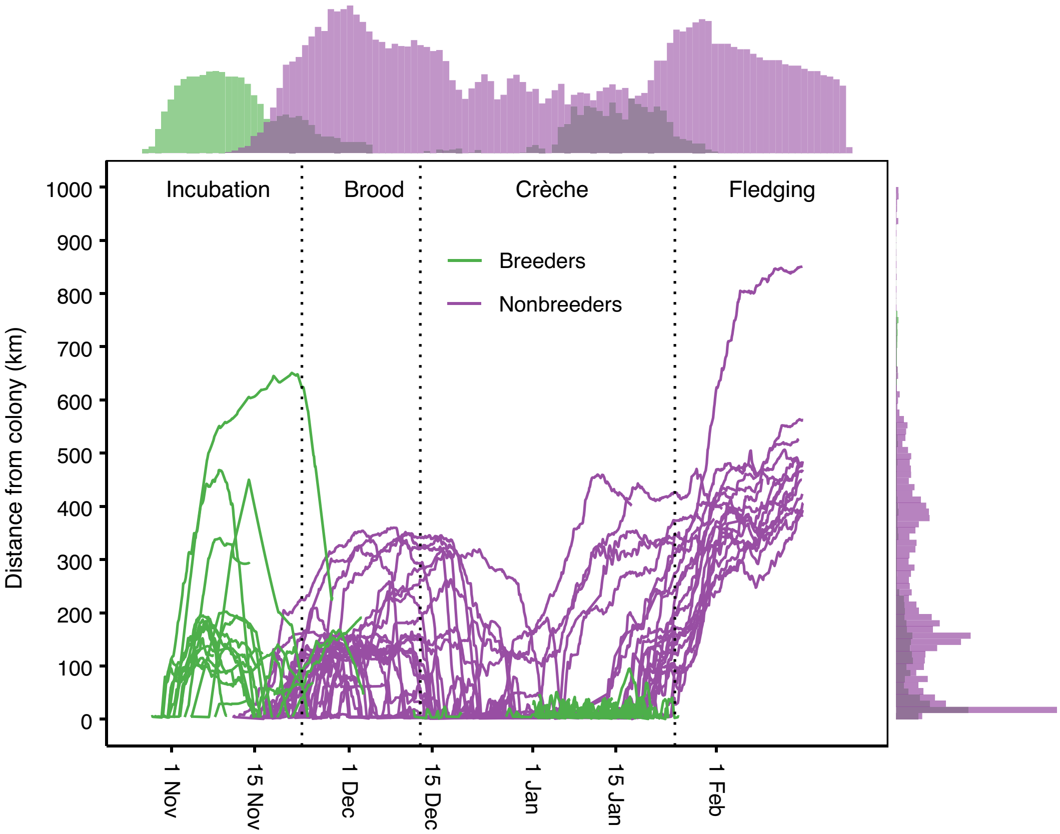

FIGURE 1 Distance from colony over time for breeding (green) and nonbreeding (purple) Adélie penguins tracked from King George Island, South Shetland Islands. The vertical dashed lines indicate the mean date of hatching, the mean crèche date, and the mean fledging date obtained from long-term phenological studies of breeders. The distributions of the data are indicated by the histograms (top: total daily discrete predicted location estimates at 2-h intervals; side: distance from colony in 10-km bins).

making relatively short trips at-sea (Appendix S1). All nonbreeders departed on premolt foraging trips into the Weddell Sea during the crèche stage (early to mid-January; Appendix S1).

Habitat use of nonbreeders

During the incubation stage, nonbreeding Adélie penguins consistently decreased move persistence in association with decreasing sea surface temperatures (Figure 2, Table 2). Movement trajectories were dominated by higher move persistence ($\gamma_t > 0.69$; the upper quartile of γ_t) as penguins traversed the comparatively deep and warm Central Basin of the Bransfield Current in the Bransfield Strait (between the South Shetland Islands and the Antarctic Peninsula). Low move persistence ($\gamma_t < 0.32$; the lower quartile of γ_t) mostly occurred in the relatively shallow and cold Weddell Sea-sourced waters near the western Antarctic Peninsula coast, and at the distal ends of foraging trips that extended into sea ice in the Weddell Sea (Figures 3 and 4).

The most parsimonious models of Adélie penguin move persistence during brood stage foraging trips included sea surface temperature and depth as covariates. Distance to the sea ice edge and sea ice concentration was included (additive to sea surface temperature and depth) in models with marginal support (Table 2). On average, nonbreeder movement trajectories were more persistent in deeper and warmer water without sea ice (Figure 2).

During crèche, the best supported move persistence models included sea surface temperature (AIC $w_i = 0.37$) or sea ice concentration and depth (AIC $w_i = 0.28$) as

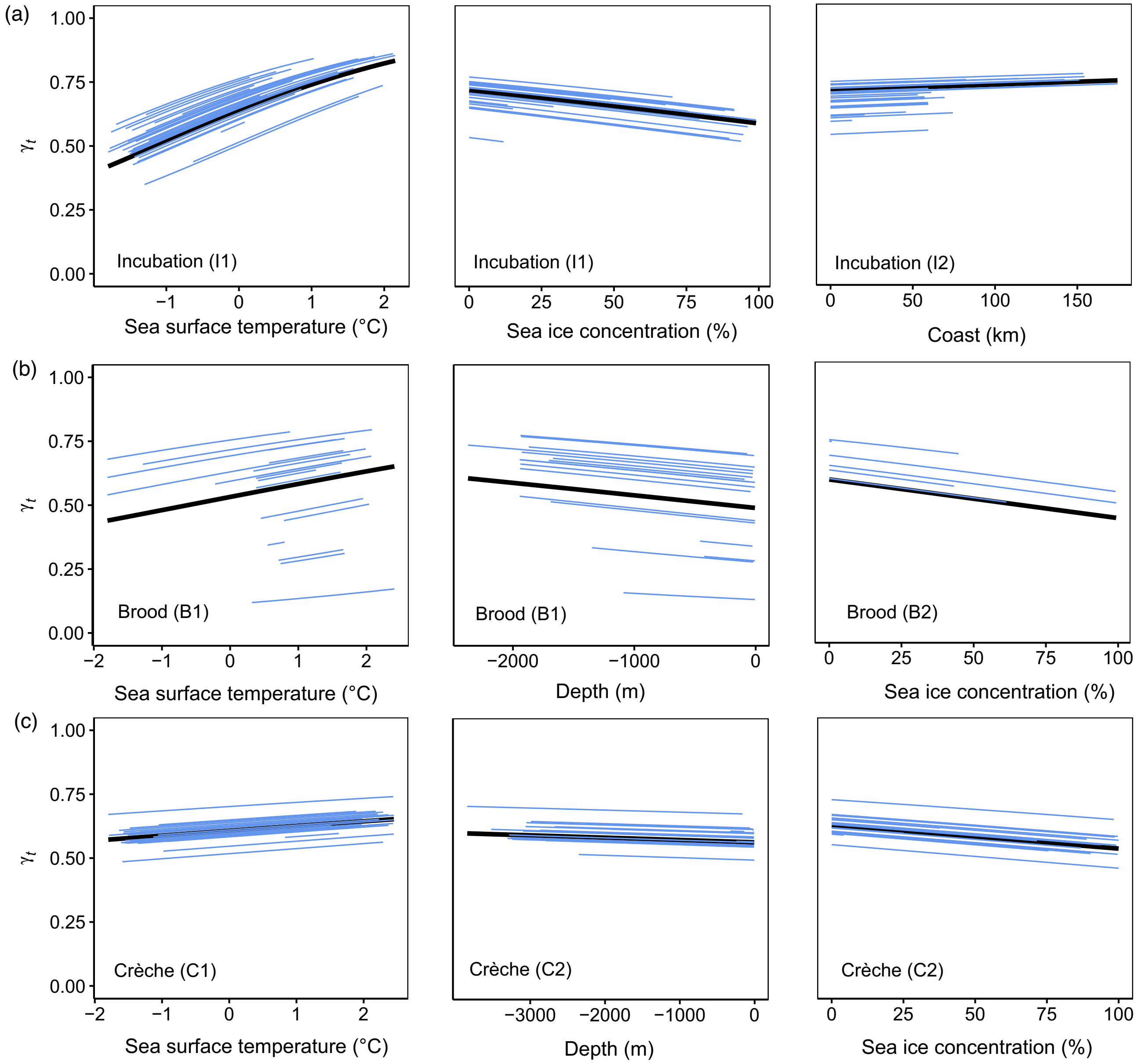

FIGURE 2 Change in move persistence (γ_t) in relation to environmental parameters for nonbreeding Adélie penguins tracked from King George Island during the incubation (a), brood (b), and crèche (c) stages of the 2016/2017 breeding season. Move persistence range from 0 ("foraging"; low directional movement persistence) to 1 ("transit"; high directional movement persistence). Fixed (black) and random (blue) effects were derived from the respective best-fitting models in Table 2 (model numbers are given in parentheses).

TABLE 2 Move persistence mixed effects model selection for Adélie penguins during the incubation, brood, and crèche stages of the breeding season

Model	Model terms	df	Deviance	ΔAIC	w_i
Incubation					
I1	sst + ice	8	−60,899.61	0.00	0.84
I2	sst + coast	8	−60,896.15	3.46	0.15
I3	sst + depth	8	−60,889.28	10.33	0.00
I4	sst	7	−60,884.54	13.07	0.00
I5	depth + ice	8	−60,885.39	14.23	0.00
I6	null	6	−60,798.64	96.98	0.00
Brood					
B1	sst + depth	8	−14,988.42	0.00	0.47
B2	depth + ice	8	−14,985.61	2.81	0.12
B3	sst + icedist	8	−14,985.26	3.16	0.10
B4	depth	7	−14,982.63	3.79	0.07
B5	sst + coast	8	−14,984.17	4.25	0.06
B6	null	6	−14,970.79	13.63	0.00
Crèche					
C1	sst	7	−61,544.57	0.00	0.37
C2	depth + ice	8	−61,546.02	0.54	0.28
C3	fsle	7	−61,541.32	3.24	0.07
C4	null	6	−61,538.67	3.90	0.05
C5	sst + fsle	8	−61,542.53	4.03	0.05
C6	sst + icedist	8	−61,541.66	4.91	0.03

Note: Model terms listed in the table were included as fixed effects; all models included individual identity as random intercepts. Models are ranked according to differences in Akaike information criterion values (ΔAIC). The degrees of freedom (df), model deviance, ΔAIC, and AIC weight (w_i; the relative support a model has from the data compared to the other models in the set) are given. Only the top 5 covariate models and the null model are shown for each breeding stage (see Appendix S5 for the full model table).

Abbreviations: coast, distance to coast; depth, ocean depth; fsle, finite-size Lyapunov exponents; ice, sea ice concentration; icedist, distance to sea ice edge; null, intercept only; sst, sea surface temperature.

covariates. The strength of the relationship between γ_t and sea surface temperature was weaker during crèche ($\beta = 0.08$, SE = 0.04) than in brood ($\beta = 0.20$, SE = 0.08) and incubation ($\beta = 0.52$, SE = 0.05), but the trend (γ_t decreasing in colder water) was consistent through all breeding stages (Figure 2).

Comparing nonbreeder and breeder space use

Breeding and nonbreeding Adélie penguins predominately headed south and southeast after leaving King George Island (Appendix S4). During incubation, the 50% UDs of both breeders and nonbreeders were concentrated in the central Bransfield Strait, with the core distribution of nonbreeders located near the Antarctic Peninsula shelf. The 95% UDs of both life history stages extended into the eastern Bransfield Strait and Weddell Sea, while single individuals traveled well west of the Bransfield Strait (Figure 5). The brood and crèche UDs of breeders covered a smaller area near the breeding colony (Table 3). Contrary to our expectations, the UD of nonbreeders also contracted during the brood, as many individuals returned to King George Island before departing on premolt foraging trips during the crèche stage (Figures 4 and 5).

The foraging ranges (95% UD) of nonbreeding Adélie penguins showed a relatively high degree of overlap (ODOI > 0.6) with those of breeders during incubation and brood, but not during the crèche breeding stage (ODOI = 0.27) (Table 3). Overlap during crèche was low because the foraging ranges of breeding birds remained small and spatially constrained close to the breeding colony, whereas nonbreeders' premolt foraging trips extended into the Weddell Sea (Figure 5, Table 3). Overlap of core areas (50% UD) was low (≤0.10) in all breeding stages. Permutation analysis showed that there was significant segregation in the spatial distribution of breeders and nonbreeders during most of the breeding season, despite areas of overlap (Table 3).

DISCUSSION

Optimal foraging theory implies that nonbreeding seabirds, which are not tied to a central place by the requirements of offspring provisioning, could be expected to preferentially occupy different foraging habitats to conspecific breeders who are providing parental care. Yet, our study is one of relatively few on the distribution and foraging behavior of nonbreeding seabirds during the breeding season (but see, e.g., Gherardi-Fuentes et al., 2019; Loredo et al., 2019; Phillips et al., 2005; Ponchon et al., 2015) and, to our knowledge, the first to investigate how the horizontal moment behavior of nonbreeding pygoscelid penguins varied during the breeding season in the context of both the environments they exploited and in their spatial distribution relative to breeding conspecifics.

We found that the horizontal movement patterns of nonbreeding Adélie penguins became more foraging-like as sea surface temperature and bottom depths decreased, and in response to increasing sea ice concentration. Throughout the entire breeding season, nonbreeders tended to transit (high directional movement) over the relatively deep Central Basin of the Bransfield Strait when departing from or returning to King George Island.

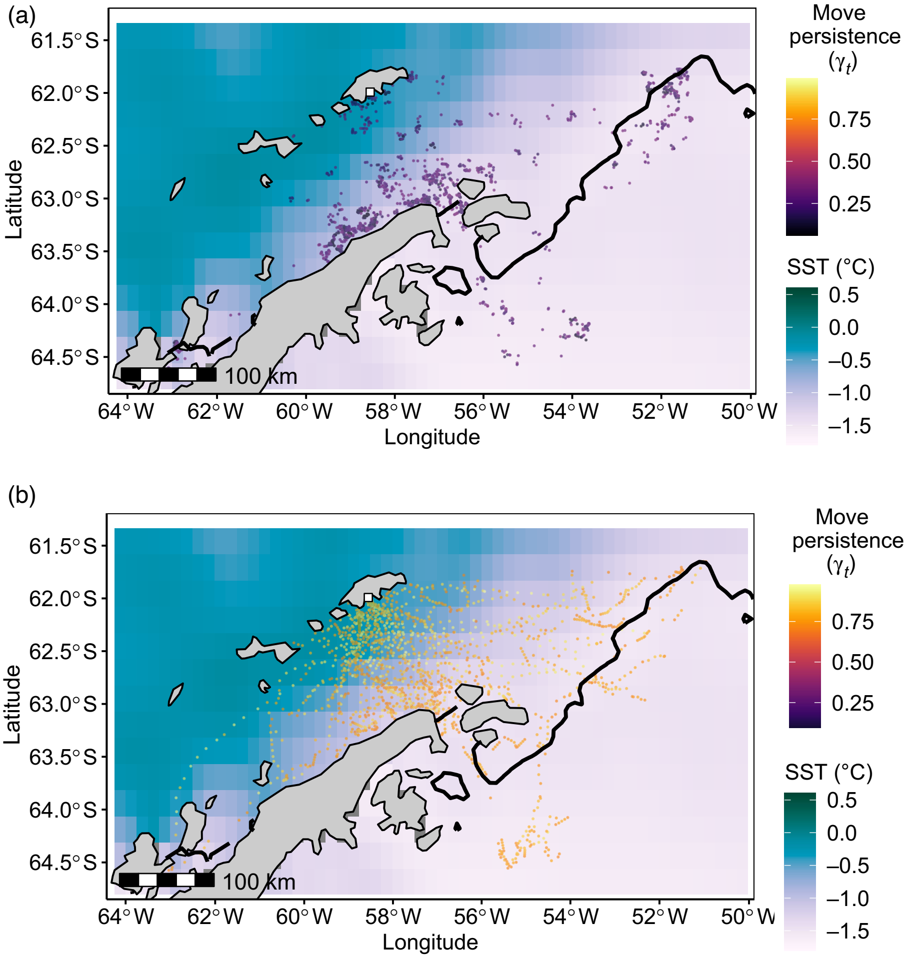

FIGURE 3 Time-varying move persistence (γ_t) of nonbreeding Adélie penguins tracked from King George Island during the incubation phase of the breeding season. The background map gives raster sea surface temperatures (SST) in degrees Celsius. The solid black line indicates the sea ice edge (15% sea ice concentration) on 30 November 2016 (the mean hatch date). (a) The lower quartile of γ_t ($\gamma_t < 0.32$), showing that low move persistence (area-restricted search behavior) mostly occurred in colder water near the Antarctic Peninsula coast and in association with low sea surface temperatures and sea ice in the Weddell Sea. (b) The upper quartile of γ_t ($\gamma_t > 0.69$) showing that nonbreeders predominantly had the highest move persistence (representing transit behavior) in the warmer waters of the Bransfield Current.

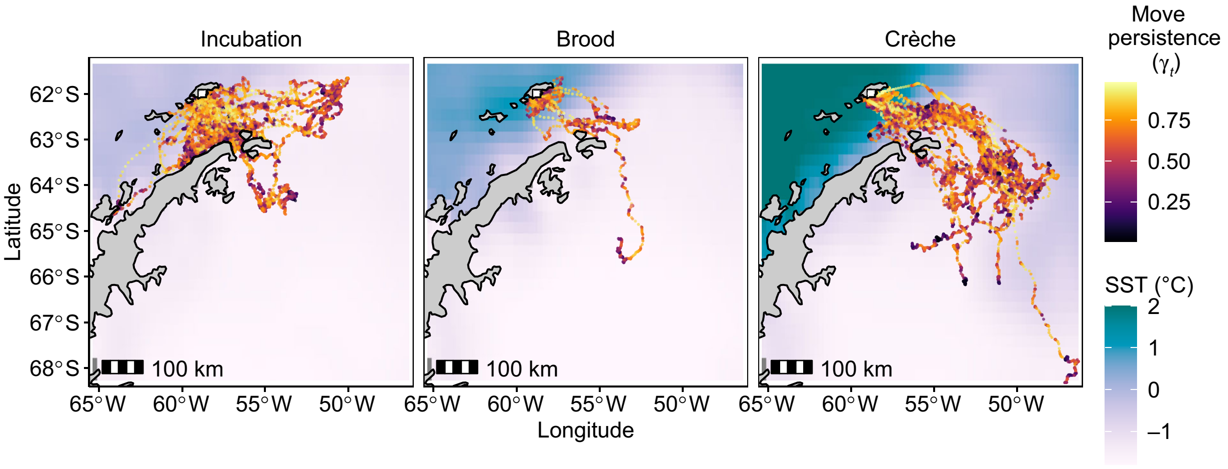

FIGURE 4 Foraging trips of nonbreeding Adélie penguins tracked from King George Island during the incubation, brood and crèche stages of the 2016/2017 breeding season. Location colors represent move persistence (γ_t) estimates ranging from 0 ("foraging"; low directional movement persistence) to 1 ("transit"; high directional movement persistence). The background map is the mean sea surface temperature (SST) per breeding stage. To improve visualization in areas of interest all temperature values higher than 2°C are given as 2°C.

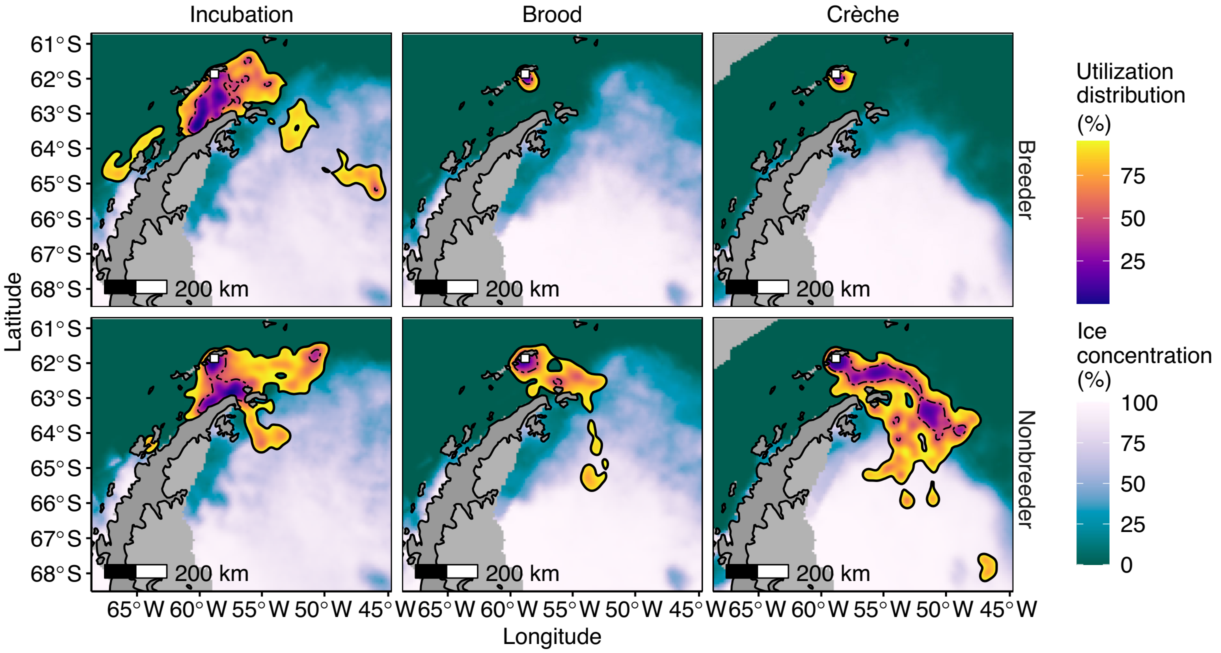

FIGURE 5 Foraging ranges of breeding (top row) and nonbreeding (bottom row) Adélie penguins tracked from King George Island, South Shetland Islands, during the incubation, brood and crèche stages of the breeding season. Kernel utilization distributions (up to 95%, with black contours at 50% [dotted line] and 95% [solid line]) shows space use and overlap of breeders and nonbreeders in each breeding stage. Admiralty Bay, King George Island, is indicated by the white square. Background maps give the mean sea ice concentration during each breeding stage.

TABLE 3 The size of the core areas (50% utilization distribution [UD]) and home range areas (95% UD) and the observed and simulated UD overlap index (UDOI) values of breeding and nonbreeding Adélie penguins during the incubation, brood, and crèche stages of the breeding season

	Area (km^2)					
Stage	**Nonbreeder**	**Breeder**	**Observed UDOI**	**Simulated UDOI (mean ± SD)**	***p***	**95% CI**
Foraging range (95% UD)						
Incubation	81,300	87,300	0.63	0.95 ± 0.10	0.007	0.003–0.014
Brood	39,375	4625	0.65	1.17 ± 0.28	0.04	0.03–0.06
Crèche	110,350	5750	0.26	1.83 ± 0.17	0	0–0.003
Core area (50% UD)						
Incubation	14,950	16,625	0.07	0.13 ± 0.03	0.016	0.009–0.03
Brood	4,500	1050	0.10	0.16 ± 0.04	0.05	0.04–0.06
Crèche	23,900	1050	0.03	0.23 ± 0.04	0	0–0.004

Note: Significant spatial segregation (at $\alpha = 0.05$) between nonbreeders and breeders was identified by comparing observed UDOI values to simulated UDOI values.

During the incubation stage, the majority of nonbreeders traveled to the southern Bransfield Strait, where their movement behavior became less persistent within the colder, Weddell Sea–sourced water of the Antarctic Coastal Current which enters the Bransfield Strait at the tip of the Peninsula, and then circulates southwestward along the northern and western Antarctic Peninsula shelf (Sangrà et al., 2011). Although there was no sea ice in the vicinity of the South Shetland Island breeding colonies, those nonbreeders traveling into the Weddell Sea encountered sea ice and displayed foraging behavior in this area. This behavior is consistent with Adélie penguins from the South Orkney Islands, which increase their area-restricted search behavior in areas with lower sea surface temperature and more concentrated sea ice during premolt foraging migrations (Warwick-Evans et al., 2019). Indeed, most available data suggest that Adélie penguins preferably forage in areas of moderate sea ice cover, such as the marginal ice zone at the sea ice edge (Le Guen et al., 2018). In contrast to the East Antarctic and Ross Sea sectors of the Southern Ocean, where unusually extensive sea ice can cause dramatic breeding failures (Ropert-Coudert et al., 2015), our results show that Adélie penguins breeding at the South Shetland Islands forage mostly in ice-free areas during the austral summer (Stammerjohn et al., 2008). While both breeders and nonbreeders are capable of targeting sea ice habitat early in the breeding season (during incubation), only the nonbreeders can continue this exploitation in the latter parts of the breeding season, when chick-rearing heighten breeders' spatial central-place foraging constraints.

The northern section of the Bransfield Strait, where breeders concentrate their chick-rearing foraging effort, and southern parts of the Bransfield Strait, where nonbreeders had core foraging areas, can differ substantially in hydrographic properties. Relatively warm and fresh water from the Bellingshausen Sea and Drake Passage enters the Bransfield Strait from the west and flows northeastward along the South Shetland Island Slope as the Bransfield Current (Siegel & Watkins, 2016). By contrast, cold and saline water originating in the Weddell Sea circulates southwestward along the southern half of the Strait (Sangrà et al., 2011). Our study contains no information on the relative distribution of Adélie penguin prey, such as Antarctic krill, in these northern and southern sections of the Bransfield Strait. However, a mixed guild of krill predators appear to target the colder waters within the southern part of the Strait, which may indicate higher availability (advection of krill into nearshore waters or shallower aggregation of krill swarms) and/or greater energy density (nutritional quality, represented by lipid content) of Antarctic krill in this area (Bernard & Steinberg, 2013; Ruck et al., 2014). Alongside the concentration of foraging activity in the southern central Bransfield Strait by nonbreeding Adélie penguins (this study), other noncentral-place foraging krill-dependent predators as well as commercial fisheries preferentially occupy the same region. The relatively shallow shelf habitat in the southern part of the Bransfield Strait is an important foraging area of male Antarctic fur seals (*Arctocephalus gazella*) satellite tracked from the South Orkney Islands (Lowther et al., 2020), nonbreeding Gentoo penguins (*Pygoscelis papua*) from the South Shetland Islands (Korczak-Abshire et al., 2021), and humpback (*Megaptera novaeangliae*) and minke (*Balaenoptera acutorstrata*) whales (Friedlaender et al., 2006; Herr et al., 2016). The distribution of the krill fishery in the Bransfield Strait varies both spatially and temporally through summer and winter (Lowther et al., 2020), but it similarly operates near the Antarctic Peninsula (Krüger, 2019), where it overlaps with the foraging ranges of krill-dependent predators (Hinke, Cossio, et al., 2017). The movement patterns of nonbreeding penguins from this study thus provide additional data to support the notion of shared habitat preferences of a mixed predator guild along the northern tip of the Antarctic Peninsula.

The multiday incubation foraging trips of breeders and the at-sea movements of nonbreeders, less affected by central-place foraging constraints, therefore allow individuals to exploit habitats in the southern region of the Bransfield Strait. By contrast, the areas over which chick-rearing adults foraged contracted to the Bransfield Current only. Because the foraging ranges of breeders provisioning chicks in brood and crèche do not always extend across different water masses, they are more susceptible to local variability in krill distribution within the Bransfield Current driven by ocean–atmospheric processes such as El Niño–Southern Oscillation (ENSO) (Loeb et al., 2009). For example, our nonbreeder data were collected during a period preceded by a sustained El Niño event during the 2015/2016 austral summer and weak La Niña conditions during the 2016 winter. Sea ice extent declined rapidly during the austral spring of 2016 and reached a record low extent beyond the foraging ranges of chick-rearing Adélie penguins from the South Shetland Islands by December 2016 (Turner et al., 2017). In general, the warmer water of the Bransfield Current extends further south during La Niña events, at which time there is also less inflow of Weddell Sea shelf waters to the southern Bransfield Strait (Ruiz-Barlett et al., 2018). This thermohaline variability in the Bransfield Strait illustrates that nonbreeding and breeding penguins, whose foraging ranges are over scale of a few tens of kilometers during chick-rearing, may not be impacted similarly by environmental variability.

Some of our results regarding comparative movement patterns between the breeder and nonbreeder life history stages were contrary to our initial expectations. During incubation, breeding and nonbreeding Adélie penguins occupied home ranges with comparable extent and had foraging trips of similar distance and duration. Like many other seabirds, breeding Adélie penguins conduct extensive foraging trips early in the season while their eggs are being incubated by their partners (Ainley, 2002). Nonbreeders followed a generally similar strategy, by returning to the breeding colony after their extended "incubation" (or more accurately post-nest failure) trips, rather than remaining at sea throughout the austral summer as one may expect from failed breeders. The nonbreeding penguins instrumented in this study thus displayed, as a group, a pronounced bimodal movement distribution with a distinct period of on-land residency in between pulses of at-sea movement during the incubation and crèche stages of breeding. Indeed, only three of the 30 nonbreeding penguins we instrumented did not return to King George Island during the brood stage. In contrast to breeders, which performed alternating short trips to sea during brood and crèche, nonbreeders often remained ashore for extended periods (up to several weeks) during the brood stage. Other studies have also described this behavior, with adult nonbreeding birds present at the breeding colony during egg laying, and again when chicks were hatching and being guarded (Ainley, 1978). Hormone cycles and nutritional status (body condition) can influence nonbreeders' foraging decisions; for example, they may return to the breeding colony to shed surplus fat as an adaptive advantage (rather than a constraint) for swimming performance (Emmerson et al., 2019). Once ashore, there is no transfer of energy from parent to offspring in nonbreeders, meaning that more assimilated energy is available for self-maintenance, thus reducing their need to forage. Nonbreeders may also remain associated with the breeding colony through behavioral mechanisms such as prospecting (social benefits that support future reproductive success) (Ainley, 2002).

The movement trajectories of nonbreeders during the crèche stage were directed and synchronized, with all birds heading southeast into the Weddell Sea, where a large amount of multiyear sea ice survive the summer melt season (Turner et al., 2020). Adélie penguins' preference to molt on sea ice was therefore the major driver of the premolt movements we observed. Postbreeding Adélie penguins tracked from the South Shetland Islands (Hinke, Cossio, et al., 2017) and the South Orkney Islands (Dunn et al., 2011; Warwick-Evans et al., 2019) behave similar on their premolt migrations, though post-successful breeders tend to start their premolt migrations later than nonbreeders.

Limitations

A key assumption in our analysis of nonbreeder habitat use is that horizontal move persistence correlated with foraging behavior. In studies of horizontal movement of marine predators, area-restricted search or low move persistence behaviors are generally thought to relate to increased foraging activity. However, in the absence of more direct data on foraging (e.g., diving behavior or animal-borne camera footage), we have to assume that foraging occurs mainly during times when penguin tracks display lower move persistence. This assumption may not always hold—breeding Adélie penguins in the Ross Sea, for example, make foraging dives throughout foraging trips and not only in areas of lower move persistence (Riaz et al., 2020). At-sea resting behavior may also lead to periods of low move persistence that do not equate to foraging behavior (Riaz et al., 2020). Some of the low move persistence locations we recorded in the Weddell Sea during crèche may, for example, be caused by nonbreeders hauling out on sea ice to rest, but teasing apart resting behavior from foraging is difficult in the absence of additional data.

We also assumed that the strength and direction of the relationship between environmental covariates and γ_t were the same across individuals (i.e., slopes were the same for all individuals). Random slope mixed effect models may better represent the among-individual variation in foraging–environmental relationships that we expect, but convergence warnings suggested that the data did not contain enough information to estimate individual slope parameters reliably.

Utilization distribution estimates are sensitive to data limitations (e.g., sample size—the number of individuals tracked and locations per individual) and modeling choices (e.g., the specification of smoothing parameters). Our sample sizes were adequate to predict the core areas of space use for breeders and nonbreeders, but more data may be needed to define the entire foraging range with confidence, especially for life history stages with larger among-individual spatial variance (Blundell et al., 2001). A limitation of our comparison of space use between breeders and nonbreeders is that the data were collected in different years. Nonetheless, we think that the breeder data captured the broad, population-level space use as it were collected over multiple years and thus incorporate temporal environmental variability which may influence foraging ranges. There was also a degree of temporal mismatch of data at a finer scale: Breeder incubation trips typically started earlier in the incubation phase than those of nonbreeders, and breeders were almost exclusively tracked in late-brood, at a time when chicks were already starting to crèche (Figure 1, Appendix S1). Space use was similar for breeders provisioning chicks in brood and crèche, and we therefore expect that the fine-scale mismatch in timing between breeders and nonbreeders will have little consequence for our conclusions.

Monitoring and management implications

Biological sentinels such as seabirds integrate information over the environment which they exploit; the spatial and temporal scales of foraging are therefore important to interpret variability in responses (Piatt et al., 2007). In breeding Adélie penguins, response parameters such as chick weight at fledging and chick diet would generally reflect mesoscale variability in the environment, that is, fluctuations in local conditions. By comparison, nonbreeding penguins have increased opportunities for foraging patch selection, allowing them to target more distant habitats (this study) or diverse prey groups (McInnes et al., 2016) relative to breeders. As such, the movement patterns of nonbreeders should provide insight into habitat preferences at larger spatial scales than breeders, that is, broadscale regional variability that could potentially be masked by provisioning constraints in breeding birds.

Knowing what constitutes important at-sea foraging habitats of nonbreeding seabirds is also fundamental to ensuring management strategies are effective to conserve all individuals with reproductive value, and not only the current breeding population. Life history stages are inextricably linked within individuals, and the movement behavior of nonbreeders can have carryover effects on their survival or reproductive performance in a subsequent season (Clay et al., 2018). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is responsible for the conservation measures that determine the use of living marine resources in the Southern Ocean (Constable et al., 2000). CCAMLR recognizes the importance of monitoring the population responses of land-based marine predators, such as Adélie penguins, as indicators of ecosystem performance (Agnew, 1997; Watters et al., 2013). The at-sea tracking data from nonbreeding adults—an important yet currently understudied demographic group—that we presented in this study will benefit monitoring and spatial management frameworks (e.g., in relation to risk assessment frameworks, the establishment of marine protected areas, or any future adaptive management framework for the krill fishery; WG-EMM, 2019) to ensure that management and conservation planning decisions better reflect spatial patterns of entire populations (Carneiro et al., 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Hinke, 2022; Lowther et al., 2021) used in the analyses are available from Zenodo (https://doi.org/10.5281/zenodo.5036339) and the NOAA National Centers for Environmental Information (https://doi.org/10.25921/vdt2-vr91).

ETHICAL STATEMENT

Nonbreeder data were collected under permits from the Polish Permitting Authority (IBB PAS permit no. 02/2016), and the Dirección Nacional del Antártico. Research at the Copacabana colony was permitted under U.S. Antarctic Conservation Act Permits (Permits 2007-003, 2011-005, 2012-005). Field protocols were approved by the University of California San Diego Institutional Animal Care and Use Committee (S05480).

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