



Using latent behavior analysis to identify key foraging areas for Adélie penguins in a declining colony in West Antarctic Peninsula

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Abstract

Adélie penguins are considered indicators of Antarctic ecosystems. Their populations have declined by more than 50% in the West Antarctic Peninsula, an area strongly affected by global warming, and that concentrates most of Antarctic krill harvesting. The use of high-resolution data to identify foraging areas regularly used by krill predators could provide valuable information for current discussions on the development of small-scale management and conservation measures for this region. We used information on the foraging trips of 57 individuals breeding in King George Island, tracked over 2019/2020, 2020/2021 and 2021/2022 breeding seasons during the chick-rearing stage, to identify their key foraging areas. Using an accelerometry-based latent behavioral analysis approach, we identified an area within 10 km of the colony consistently used by over 60% of the population throughout and between seasons. We also observed that almost 20% of the population uses the area near a seamount located 35 km from the colony for foraging, mainly during the late guarding phase when chick energy demands are highest or the effects of prey depletion might become more evident. The distances and duration of trips and the area explored increased as the season progressed and varied between seasons, consistent with annual differences in krill availability observed in the region. Foraging dives comprise roughly 40% of the dives performed during foraging trips, irrespective of the stage of the chick-rearing period, or the season analyzed. Our results emphasize the need to understand how variability in environmental conditions, prey availability, and energetic demands affect how predators use space, and the role that bathymetric features might play in providing reliable foraging grounds, for penguins, in a rapidly changing region.

Keywords CCAMLR · Bransfield Strait · Bio-logging · Antarctica · Ardley Island · Ecosystem management · Foraging ecology

Introduction

Monitoring marine predators at sea, such as penguins, can identify areas of ecological importance. Areas with high concentrations of predators often indicate a high biodiversity

and biomass at lower trophic levels and are, therefore, regions that may require special management (Hindell et al. 2020; Ropert-Coudert et al. 2020). With nearly 4 million breeding pairs around Antarctica, Adélie penguins (*Pygoscelis adeliae*) are one of the most important and best studied predators in the Southern Ocean (Ancel et al. 2013; Lynch and LaRue 2014). As a key predator of krill and with a strong dependence on the sea-ice environment, the Adélie penguin has been considered an indicator species, being highly sensitive to changes in the marine ecosystem (Boersma 2008; Hinke et al. 2014; Ropert-Coudert et al. 2018).

In western Antarctic Peninsula (WAP), one of the polar areas most affected by global warming, Adélie penguin populations have declined by more than 50% since the 1970s (Trivelpiece et al. 2011; Lynch et al. 2012). In contrast, East Antarctica has experienced a 1.5% increase in sea-ice extent (Michel et al. 2019), with Adélie penguin populations

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stable or slightly increasing (Southwell et al. 2015). Penguin population decline in the WAP has been linked to large-scale changes in the biomass of Antarctic krill (*Euphausia superba*; Trivelpiece et al. 2011). Antarctic krill is being affected by ongoing environmental changes, with a decrease in density and mean size, and a southward contraction in the southwest (SW) Atlantic sector associated with warm, windy and cloudy weather, and a reduction in sea ice (Atkinson et al. 2019). This is noteworthy because further environmental changes could cause additional range contractions and decrease in krill biomass along the WAP (Klein et al. 2018; Atkinson et al. 2019), which could lead to a mismatch between peak food availability and breeding season, increasing penguin foraging efforts and decreasing reproductive success (Cimino et al. 2023; Salmerón et al. 2023).

In addition, the commercial catch of krill has increased in recent years in the SW Atlantic sector (FAO statistical Area 48) reaching in the 2019/2020 season the highest level recorded (CCAMLR 2021). Catches are also intensifying, with the fleet repeatedly visiting fishing hotspots, particularly close to predator breeding colonies in the Bransfield Strait and South Shetland Islands (Santa Cruz et al. 2018; Trathan et al. 2018). Hinke et al. (2017) highlight that direct overlap of krill-dependent predators with the krill fishery on small spatiotemporal scales is relatively common throughout the WAP, and several works have pointed out the need for a krill exploitation framework that ensures small-scale precautionary protection to minimize negative effects on dependent predators (Santa Cruz et al. 2018; Watters et al. 2020; Trathan et al. 2022).

During the breeding season, Adélie penguins are central-place foragers, as they must frequently return to the colony to incubate their eggs or feed their offspring. These seabirds change their foraging behavior in response to environmental variability, fluctuations in prey availability and chick provisioning requirements throughout the season (Clarke et al. 2006; Ballard et al. 2010). The foraging strategies of Adélie penguins have been well studied in the WAP (Wilson et al. 1994; Wilson 2002, 2010; Fraser and Hofmann 2003; Cimino et al. 2016; Hinke et al. 2017; Warwick-Evans et al. 2022). In general, they tend to forage offshore in the upper 50 m of the water column (Trivelpiece et al. 1987; Wilson 2010; Cimino et al. 2016), and unlike colonies in East Antarctica and the Ross Sea, the diet of the colonies in the WAP and the South Shetland Islands is dominated by Antarctic krill throughout the breeding season (Gorman et al. 2014; Negrete et al. 2016; Herman et al. 2017; Juárez et al. 2018; Pickett et al. 2018). However, considerable colony-specific differences are evident in Adélie penguin foraging behavior. The variability in abundance and distribution of prey driven by regional variation in physical and environmental features, such as sea ice cover near the colonies or different bathymetric features (e.g. submarine canyons), influences differences

in foraging ecology between penguin populations along the WAP (Fraser and Trivelpiece 1996; Santora and Reiss 2011; Cimino et al. 2016; Nardelli et al. 2021).

Given this scenario of rapid climate change and intensification of krill fisheries in the WAP, monitoring Adélie penguins foraging behavior may improve our understanding on how predators respond to inter-annual variation in krill availability. Furthermore, the use of high-resolution data, such as accelerometers, to identify foraging areas regularly used by these krill predators, could provide valuable information for the development of small-scale management and conservation measures for this region. This is particularly relevant in a warming Antarctic Peninsula scenario (Siegert et al. 2019), where the impacts of ongoing decrease in sea-ice habitat and southward shifts in marine species distributions are exacerbated by the effects of marine resource extraction.

Thus, the objective of this study is to describe the foraging behavior and identify foraging areas used by Adélie penguins breeding in Ardley Island, in King George Island/Isla 25 de Mayo, South Shetland Islands, an area free of sea-ice throughout the summer. We analyze changes in penguins foraging behavior during the chick rearing stage, a highly demanding period for breeding adults due to the increasing energetic requirements of chicks and foraging constraints as central place foragers (Bevan et al. 2002; Clarke et al. 2006). As chicks grow, the energy needs of adults and the tolerance of chicks to fasting also change, affecting adult foraging behavior throughout the breeding season (Widmann et al. 2015; Riaz et al. 2020; Phillips et al. 2021). To ensure regular feeding of offspring, adults should seek to minimize time away from the colony prioritizing the exploitation of food resources available nearby. However, when prey availability in the vicinity of the colony is low, they have to increase the time away from the colony as they forage in more distant areas (Clarke et al. 2006). Therefore, we expect foraging effort (e.g., trips distances or duration) to increase as the season progresses, or in years with reduced krill availability, with foraging areas' location varying accordingly. Identifying foraging areas that are regularly used by penguin colonies enables adopting spatially explicit conservation measure aimed at avoiding overlap between fisheries and predators during this key stage of the annual cycle.

Materials and methods

Study area

Ardley Island (62°13' S, 58°56' W), in the southwest of King George Island/Isla 25 de Mayo, South Shetland Islands (Fig. 1), is an Antarctic Specially Protected Area (ASPA N° 150), a CEMP (CCAMLR Ecosystem Monitoring Program) site, and one of the few areas in Antarctica where

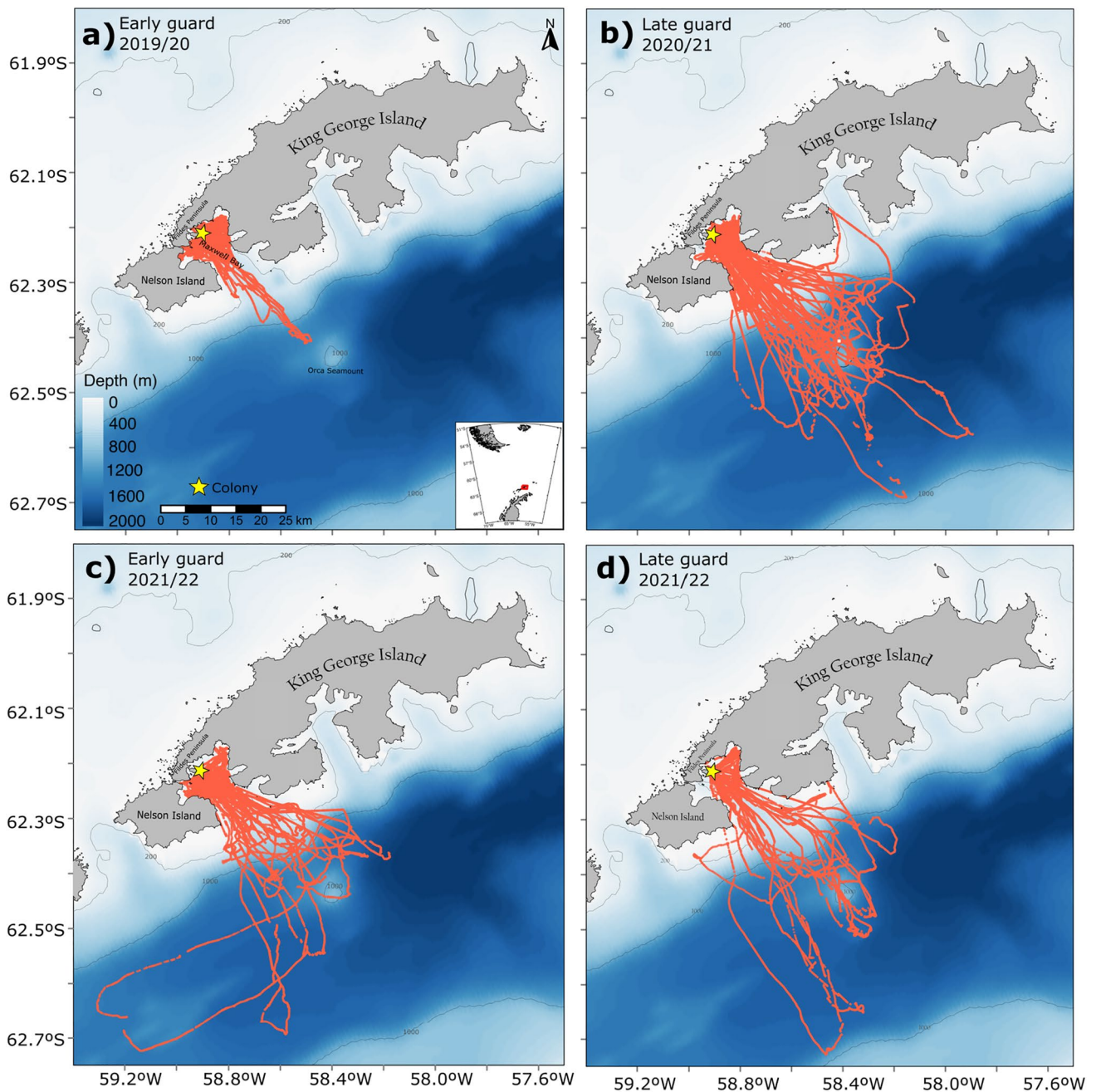


Fig. 1 GPS tracks of Adélie penguins breeding in Ardley Island (yellow star), King George Island, South Shetland Archipelago, Antarctica, during the early and late guard over three season (2019/20 –

2021/22). Inset panel in a) shows the location of King George Island (red square) in the northwest of the Antarctic Peninsula

the three pygoscelid penguin species breed sympatrically (Braun et al. 2017). Breeding population size and breeding success has been monitored since the 1980s. According to Braun et al. (2017), the numbers of breeding pairs of Adélie penguins have decreased by more than 30% since counts began, reaching the minimum of 184 breeding pairs in the 2022/2023 season (this study). In line with population trends at other colonies in the region, the number of breeding

pairs of chinstrap penguins at Ardley Island has declined by more than 90%, with a total of only six breeding pairs in the 2022/2023 season. In contrast, the number of gentoo penguins increased by over 80% during the same period, with a total of 8763 breeding pairs in the same season (this paper). Other Adélie, chinstrap and gentoo colonies in the vicinity of the study site (i.e., in Maxwell Bay) include: Narębski Point with 2918 chinstrap and 2604 gentoo breeding pairs (Lee

et al. 2021); Duthoit Point with 1828 gentoo penguin breeding pairs (Coria et al. 1995); Stranger Point with 3703 Adélie and 5383 gentoo breeding pairs (Juárez et al. 2015, 2020).

Field procedure (Deployment of data loggers)

The study was conducted over three breeding seasons: 2019/2020, 2020/2021 and 2021/2022. Axy-Trek (70×40×15 mm, 69 g; TechnoSmart, Italy) loggers including GPS, accelerometer, and both pressure and temperature sensors were deployed on adult Adélie penguins rearing chicks. To account for the increasing demand for food by chicks as they grow and its possible influence on adult foraging behavior (Widmann et al. 2015), we divided the chick rearing period into two stages: early guard and late guard. Due to logistical limitations, not all stages could be sampled equally in the three years of the study, so data were obtained for early guard stage during 2019/2020 and 2021/2022, and for late guard during 2020/2021 and 2021/2022 breeding seasons (See Table 1). The chick rearing period (i.e., “guard”) stage lasts about 22 days (Black 2016), with hatching beginning in late November-early December on King George Island/Isla 25 de Mayo (Juárez 2013; Handley et al. 2021). During the study period, the peak of hatching in the studied colony occurred between December 4 and 6 (this study). Here we defined the early guard stage as approximately the first half of the chick rearing period (between December 6 and 23) and the late guard as the second half

of the period and just before the start of crèche (between December 24 and January 6).

We captured only one member of the pair in nests with two chicks, mainly by hand, with the occasional aid of a long-handled net. We also captured chicks during adult handling to protect them from predators and measured their body mass with a Pesola spring balance. We took care to minimize stress to the captured adults by covering the head during handling and ensuring that handling time was always below 20 min. The recorders were attached on the birds’ lower back feathers using Tesa® 4651 tape (Wilson et al. 1997). The loggers used represent 1.6% of the body mass of an adult Adélie penguin (mean for Ardley Island 3847 ± 392.3 g; this study). The loggers were programmed to record a position every 5 min, pressure (in millibars) at 1 Hz and acceleration along the 3 body axes of the penguins: longitudinal (surge), dorso-ventral (heave) and lateral (sway) at 50 Hz. The tagged birds were recaptured in the nest after 3–7 days and the loggers were removed to access recorded data. After device removal, body mass of the adults and chicks were measured using a Pesola spring balance.

GPS and dive data analysis

GPS data from a total of 205 trips, undertaken by 57 birds with each bird making between two to nine trips, were analyzed using the R software (version 4.1.3; R Core Team

Table 1 Trip and dive characteristics (mean ± SD) of Adélie penguins breeding in Ardley Island during early and late guard between 2019 and 2022. The (*) indicates that there are significant differences between early and late guard. Significant differences between seasons within the same guard period are shown in bold. UDs were calculated using h-value = 1.67 km

	Early Guard		Late Guard	
Season	2019/2020	2021/2022	2020/2021	2021/2022
Date of sampling	06 dec-15 dec	09 dec-23 dec	24 dec-02 jan	24 dec-06 jan
Trip parameter				
N° Trips (N° ind)	67 (19)	52 (15)	59 (16)	27 (7)
Trip duration (h)*	8.63 ± 3.66	18.26 ± 11.26	20.85 ± 11.01	22.55 ± 11.44
Max. distance from colony (km)*	6.6 ± 5.42	15.21 ± 14.76	25.16 ± 17.92	23.77 ± 19.00
Total distance traveled (km)*	19.33 ± 12.33	43.33 ± 36.26	64.66 ± 40.40	62.47 ± 42.23
Max. trip depth (m)*	73.14 ± 17.24	86.35 ± 19.95	90.85 ± 14.73	85.50 ± 21.03
Home range (95% UD) (km ²)*	126.25 ± 61.68	361.58 ± 270.51	587.78 ± 215.56	580.40 ± 231.62
Home range (90% UD) (km ²)*	100.69 ± 51.48	293.36 ± 226.59	490.67 ± 185.41	482.65 ± 198.17
Home range (50% UD) (km ²)*	31.59 ± 15.99	80.40 ± 75.91	149.65 ± 66.88	150.59 ± 72.24
Dive parameter				
N° of dives	20,342	31,625	37,119	17,396
Dive duration (s)	54.89 ± 6.13	61.86 ± 7.23	71.79 ± 7.73	63.26 ± 7.01
Depth (m)	18.84 ± 5.28	21.50 ± 6.66	25.03 ± 6.42	21.45 ± 6.03
Bottom time (s)	28.36 ± 3.10	33.20 ± 2.99	36.50 ± 3.16	34.91 ± 4.21
N° of wiggles	4.67 ± 0.58	5.10 ± 0.59	5.47 ± 0.67	5.25 ± 0.94
Proportion of bottom time	0.52 ± 0.07	0.55 ± 0.08	0.52 ± 0.07	0.56 ± 0.04
Dive frequency*	35.90 ± 9.34	34.06 ± 10.74	30.58 ± 9.63	29.16 ± 10.16
Proportion of dives	0.53 ± 0.09	0.55 ± 0.12	0.58 ± 0.14	0.49 ± 0.15
Dive efficiency	0.27 ± 0.06	0.30 ± 0.08	0.30 ± 0.09	0.28 ± 0.09

2022). Excessive points recorded before departure and after arrival at the colony were manually removed, retaining only five points located at the colony in each case. To filter possible erroneous location estimates we removed points leading to horizontal speeds above $7 \text{ km}\cdot\text{h}^{-1}$. This velocity threshold was chosen based on our data and less than 1% of the records were above that value (Fig. S1). For each individual, foraging trips were defined from the time the birds moved more than 50 m from the colony to the sea until the time they were within 50 m of the colony again. The number of trips, and the date and time of the start and end of each trip were calculated for each individual. With this, three representative parameters of foraging effort were also calculated for each trip: total trip duration, total trip distance (i.e. the cumulative horizontal distance between all GPS locations per bird per trip), and maximum distance to the colony (i.e. the straight line distance between the colony and the most distal point of a trip).

Dives were analyzed using the software Igor Pro Version 6.37 (Wavemetrics). Pressure (mBar) was converted to water depth (m) as $\text{water depth} = (\text{pressure} - \text{atmospheric pressure})/100.45$. Atmospheric pressure is estimated as the mode of the pressure data (around 1000 mBar). The surface line (0 m) was visually checked and corrected manually when needed. Dives were defined as the period between the time the birds descended from the water surface and the time when they returned to it. Only dives deeper than 1 m were included due to possible measurement error in instruments and surface waves (Takahashi et al. 2003; Kato et al. 2009). For each dive, different parameters were calculated: dive depth (m) (determined as the deepest point of the dive), total dive duration (s), bottom time duration (s) (start and end of bottom time were defined as the first and last time in a dive when the depth change rate was $<0.25 \text{ m}\cdot\text{s}^{-1}$) and number of wiggles (number of vertical undulations during the bottom phase, i.e. the point of inflexion in the dive profile). Maximum depth recorded on each trip was also calculated. The grand mean \pm SD of these parameters per trip was calculated for each stage and season using the *R effectsize* package (Ben-Shachar et al. 2020).

For each trip we calculated the proportion of trip diving (total time diving divided by trip duration), the proportion of time spent in the bottom phase (total time in bottom diving divided by total time diving), dive frequency (number of dives divided by trip duration) and dive efficiency (total time in bottom diving divided by trip duration). We then matched the dive data with GPS locations, using date and time information. To do this, we allocated a location to each dive by linearly interpolating the timestamp at the beginning of each dive event with the closest GPS locations recorded before and after the dive (Kokubun et al. 2010). The mean time interval between records of GPS locations was $6.9 \pm 0.3 \text{ min}$. We used 500-m resolution bathymetry data obtained from

the General Bathymetric Chart of the Oceans (GEBCO Compilation Group 2020).

Finally, for each individual we estimated their utilization distributions (UDs) by calculating fixed kernels using the *adehabitatHR* package (Calenge 2006). To calculate h-values, data on all tracks of all individuals monitored during the study period were pooled together. Geographic positions were transformed into stereographic coordinates to calculate the size of UD for different isopleths. We used the ‘ad-hoc’ method (Schuler et al. 2014) to calculate kernels’ bandwidth (h). Initial estimation of the 90% UD was calculated using the reference bandwidth (i.e., the href value, calculated on the basis of the number and spatial variance of all tracking locations, assuming bivariate normality). A sequence of 90% UD was then calculated by reducing the h-value by 5% in successive steps, until the 90% contour fractured into two or more polygons. The ad-hoc value thus corresponds to the smallest h-value calculated that retains the number of polygons initially calculated using the href value.

Identify key foraging areas

To identify key foraging areas, we use the approach developed by Chimienti et al. (2016, 2022) for characterizing latent behaviors to determine in which dives penguins are attempting to capture prey. Using this approach, we first identify all dives recorded within each foraging trip in which penguins seem to be attempting to catch prey, and then identify the areas where these dives concentrate, integrating information on all trips and individuals studied throughout the whole study period. As a first step for the analysis, accelerometer data were checked and records subsampled at 25 Hz, following Chimienti et al. (2016). We used the depth data to retain only the data during the underwater activity of each individual. Only dives deeper than 2 m were considered, to avoid measurement errors and behaviors at the sea surface that do not correspond to foraging activities (foraging vs commuting). We then used Chimienti et al. (2016, 2022) method for analyzing accelerometry data to automatically identify behavioral modes and individual behaviors, in species moving in two or three dimensions. The method uses the unsupervised machine learning algorithm Expectation Maximization to find maximum likelihood solutions for mixture models with latent variables, and was implemented using the R package *RMixmod* (Biernacki et al. 2006). Based on the input variables, the model automatically defines clusters without a priori information. The model is tested with different numbers of clusters (from three to eight for the diving part in Chimienti et al. 2022). For the specific case of the Adélie penguins, the optimal number of clusters was four, and was selected as a compromise between ecological meaning of these clusters and model performance (see Chimienti et al. 2022). The ecological meaning of each

cluster is inferred by the researcher based on the knowledge of the study species and by visualizing the results of each run. These were: descending phase, deep searching phase, chasing/catching events and ascending phase. As the depth data used to describe the dive profiles were recorded every 1 s, we classified each depth record as corresponding to either a capture attempt or not, based on whether more than 50% of the accelerometer records within that second were classified as chasing/catching events by the model, or not. We then used that information to classify dives as either foraging dives (i.e., where penguins were attempting to capture prey), or not. We aimed to discriminate foraging dives from dives where animals are not hunting, or where the scarce numbers of capture attempts rather reflect casual encounters with prey. We defined foraging dives as those where at least 5 s of the diving cycle were classified as capture attempts. The 5 s criterion is an arbitrary limit chosen as a rough proxy of the mean number of krills that have to be captured by penguins in foraging dives, to fulfill daily energetic demands. The reasoning supporting this value is as follows: breeding Adélie penguins require approximately 800–1200 g of krill daily (Watanabe et al. 2013; Warwick-Evans et al. 2022), they capture 300–400 g of krill in each foraging trip (Watanabe et al. 2013; Juárez et al. 2018), individual krill weight is close to 0.4 g on average (Watanabe et al. 2013; Juárez et al. 2018), Adélie penguins have been observed to capture up to two krill per second in swarms (Watanabe et al. 2013), and our data suggest that in our study area foraging trips last 8–22 hs, diving frequency is close to 30 dives hour⁻¹, and in roughly 50% of the dives penguins do not attempt to capture prey. This suggests that in all other dives individuals need to devote on average at least 2 to 5 s of the dive to food ingestion, if energetic demands are to be met at the end of the day. We thus consider foraging areas as those that concentrate dives that have a potential significant contribution to individuals' energetic demands (i.e., dives where at least 5 s of the diving cycle were classified as capture attempts).

For foraging dives the following parameters were determined: dive duration, dive depth, bottom time duration, number of wiggles, foraging frequency (number of dives with at least 5 capture attempts divided by trip duration), and maximum depth recorded per trip. Values per stage and season are presented as grand mean \pm SD, and were calculated as described before.

To identify foraging areas we used the *track2KBA* package (Beal et al. 2021) for R. Only positions of foraging dives that met the criterion established in the previous step were included in the analyses (Fig. S3 shows negligible changes in these areas when more restrictive values are used to define foraging dives). For each individual, the 50% isopleth of the UD were calculated with the h-value calculated using the ad-hoc method described before. To identify foraging areas for the colony, individual UD overlap was estimated for

the whole study period using the package's 'findSite' function. Following Beal et al. (2021), for each 0.16 km² cell of the study area we calculated the percentage of individuals using that cell (i.e., cells used by an individual are those included within the individuals' 50% isopleth). We estimated the representativeness of our samples with respect to the colony using the function *repAssess*. The function iteratively selects sub-samples of individual tracks, averages them into a pooled UD and outlines a desired quantile, and then calculates the proportion of out-of-sample tracking locations within the resulting area (i.e., the 'inclusion rate'). This proportion approximates the specified UD quantile when the tracked sample is fully representative (see Beal et al. 2021 supporting information for further details). Representativeness values were estimated after 100 iterations.

Statistical analyses

To test for differences between stages and seasons in the foraging parameters analyzed we used different statistical models, to account for differences in the response variables and their effects on models assumptions. In each model, the season (early 19/20, early 21/22, late 20/21, late 21/22) or stage (early, late) was considered as an independent factorial variable and the individual (ID) as a random effect to account for repeated measures of the same individual. Season is a combination of year and stage, as it was not possible to sample in both stages during the three breeding seasons as e.g., COVID restrictions precluded early arrival to the study area in 2020. For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. When these did not meet models' assumptions, a different model was selected. When significant differences between stages or seasons were detected, we performed Tukey's post hoc tests using the *multcomp* package (Hothorn et al. 2008).

For the only continuous response variable with normal distribution (maximum depth) we used linear mixed models (LMM) implemented in the R package *lme4* (Bates et al. 2015). Continuous response variables that did not present a normal distribution (trip duration, maximum distance from colony, total distance traveled and dive frequency) were log-transformed. For the response variables that did not fit a normal distribution due to a high number of observations with low values (dive duration, depth and bottom time), we compared between seasons and stages using generalized linear mixed models (GLMM) using the Tweedie distribution family (with the index of power variance function selected according to response variable distribution) and a log-link function (Faster and Bravington 2013), implemented in the *lme4* and *statmod* packages. For continuous proportion variables (proportion of bottom time, proportion of trip diving

and dive efficiency) we used GLMM with the beta binomial distribution family and for the count response variable (number of wiggles) we used GLMM with negative binomial distribution because of overdispersion, using the *glmmTMB* package (Brooks et al. 2017). In addition, we compared differences in home range area (km²) at 95%, 90%, and 50% isopleths using Analyses of Variance (ANOVA).

For foraging dives we also made comparisons between stage and season. The variables dive duration, depth (log transformed), maximum depth, bottom time and foraging frequency were modeled using LMM and the number of wiggles through a GLMM with negative binomial distribution. In all cases, the season or stage was considered as an independent variable and the individual as a random effect. In all the analyses, when significant differences occurred between seasons, Tukey's post-hoc tests were performed using the 'glht' function from the *multcomp* package (Hothorn et al. 2008), in order to assess whether differences were observed within stages.

Results

Tracking data from 57 individual birds from Ardley Island over three breeding seasons, provided information on 205 foraging trips, 106 482 dives, and 45 179 foraging dives with at least five capture attempts (Table 1, 2 and Table S1). We found significant differences in foraging trip characteristics as the season progressed. During the late guard trips lasted longer than during early guard (10.99 ± 0.07 h vs. 19.28 ± 0.09 h; LMM, $F = 24.38$; $p < 0.001$; Fig. 2), total distance traveled was more than double during late guard than in early guard (22.41 ± 0.09 km vs. 53.02 ± 0.11 km; LMM, $F = 34.75$; $p < 0.001$; Fig. 2), as well as maximum distance to the colony (7.12 ± 0.10 km vs. 18.48 ± 0.12 km; LMM, $F = 34.95$; $p < 0.001$; Fig. 2), and the maximum depth recorded was deeper during late guard than in early guard (78.75 ± 2.18 m vs. 90.31 ± 2.61 m; $F = 11.57$; $p < 0.01$; Fig. 2). The 50, 90 and 95% UD were also significantly

larger during the late guard (LM, $F = 45.66$; $F = 45.91$; $F = 45.14$; $p < 0.001$, respectively; Fig. 2). For these estimates h-value was set at 1.67 km. Finally, the frequency of dives was lower during the late guard (33.74 ± 0.03 vs. 28.94 ± 0.04 ; LMM, $F = 7.33$; $p < 0.01$; Fig. 3). No other dive parameters showed significant differences between stages (Table 1 and S3, Fig. 3). The indicated values are the mean and standard error for each parameter.

We also found significant differences in foraging trip characteristics between seasons. During the early guard in the 2019–2020 season, Adélie penguins undertook shorter trips in terms of total distance traveled (16.08 ± 0.11 km vs. 33.75 ± 0.12 km; LMM, $F = 22.88$), maximum distance (5.23 ± 0.13 km vs. 10.45 ± 0.14 km; $F = 18.38$; $p < 0.001$) and duration (8.04 ± 0.07 h vs. 16.04 ± 0.08 h; LMM, $F = 26.83$; $p < 0.001$) than at the same stage in the 2021–2022 season (Fig. 2). Similarly, the 50, 90 and 95% UD were smaller (LM, $F = 22.23$; $F = 28.56$; $F = 28.75$; $p < 0.001$, respectively), and the maximum depth recorded was shallower (75.52 ± 2.64 m vs. 86.66 ± 2.97 m; LMM, $F = 8.90$; $p < 0.001$; Fig. 2). There were no significant differences between the same stage in different seasons for the other parameters (Table 1 and S3, Fig. 3). The indicated values are the mean and standard error for each parameter.

Foraging dives of Adélie penguins were restricted to the vicinity of Ardley Island and comprise roughly 40% of the dives penguins perform during their foraging trips (Fig. 4 and Table 2). Figure 5 shows the areas of overlap of the 50% UD of all the individuals tracked during the study period (for the whole colony h-value = 1.67 km). Representativeness of these individuals with respect to the whole colony was estimated in 98%. Only 0.16 km² cells where the 50% UD of at least 10% of the individuals studied overlap are shown.

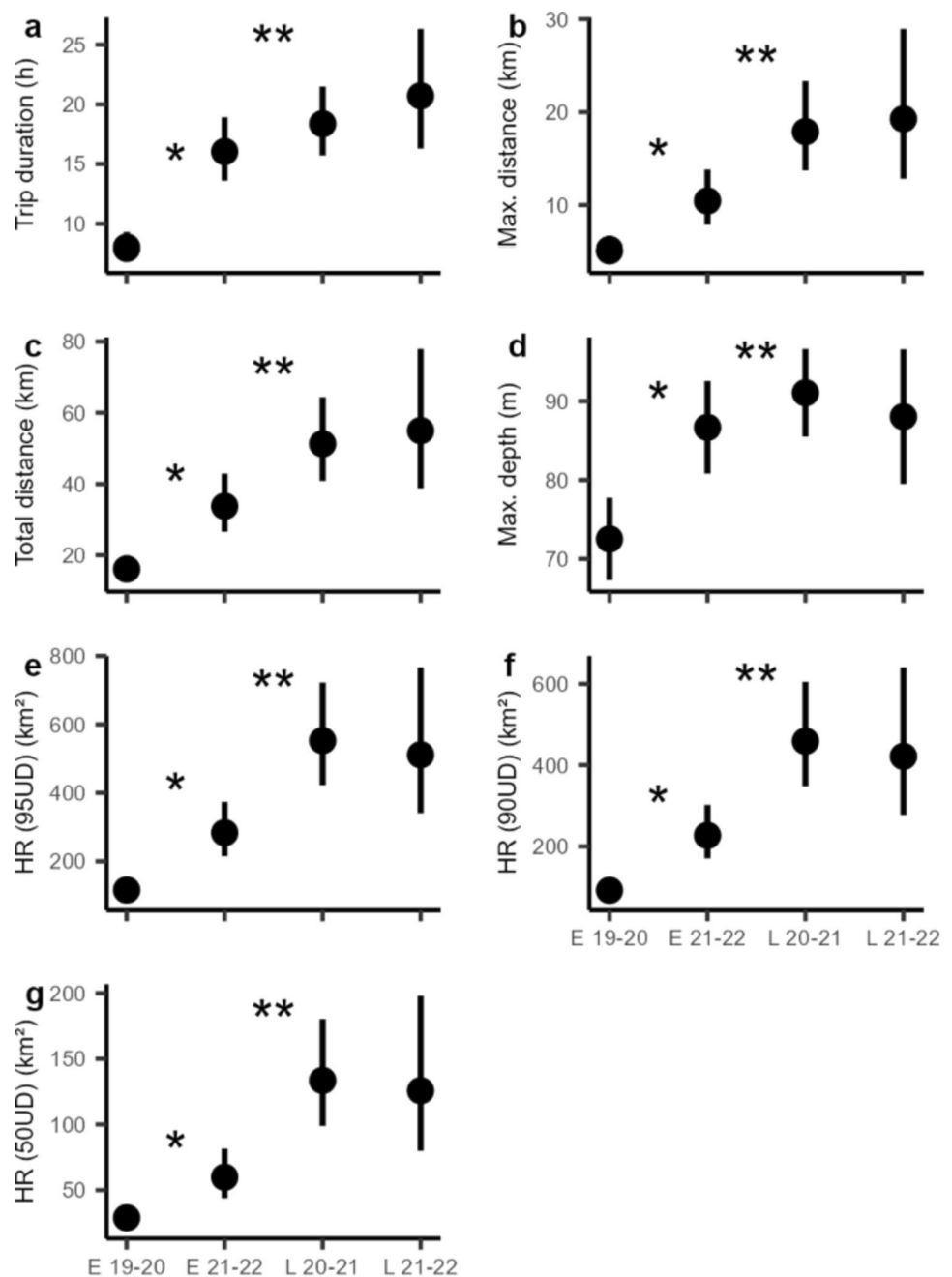
There were significant differences between foraging dive characteristics during the early and late stages. During the late guard foraging dives were deeper (26.56 ± 0.04 m vs. 33.07 ± 0.05 m; LMM, $F = 12.26$; $p < 0.001$), the maximum depth was deeper (78.54 ± 2.14 m vs. 90.28 ± 2.57 m; LMM, $F = 12.28$; $p < 0.001$), lasted longer (89.62 ± 2.08 s vs.

Table 2 Foraging dives characteristics (mean \pm SD) of Adélie penguins breeding in Ardley Island during early and late guard between 2019 and 2022.

	Early Guard		Late Guard	
	2019/2020	2021/2022	2020/2021	2021/2022
Season	2019/2020	2021/2022	2020/2021	2021/2022
N° of dives	8246 (40.5%)	13,708 (41.3%)	17,124 (46%)	6101 (35%)
Dive duration (s)*	85.12 \pm 6.44	96.63 \pm 6.50	100.25 \pm 5.73	106.52 \pm 8.71
Depth (m)*	34.04 \pm 5.13	36.73 \pm 6.06	39.71 \pm 4.62	44.72 \pm 5.23
Max.trip depth (m)*	73.07 \pm 17.31	85.99 \pm 19.77	90.85 \pm 14.73	85.50 \pm 21.03
Bottom time (s)*	41.85 \pm 2.98	49.94 \pm 2.95	48.23 \pm 2.75	51.75 \pm 5.06
N° of wiggles	7.41 \pm 0.60	7.77 \pm 0.66	7.95 \pm 0.58	8.54 \pm 1.12
Foraging frequency	15.00 \pm 4.61	16.08 \pm 5.66	15.27 \pm 4.75	11.42 \pm 5.60

The (*) indicates that there are significant differences between early and late guard. Significant differences between sampling seasons within the same guard period are shown in bold

Fig. 2 Characteristics of the foraging trips of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019–2020 and 2021–2022: E 19–20, E 21–22; late guard 2020–2021 and 2021–2022: L 20–21, L 21–22. Mean and SE (standard error) calculated from model outputs: a) Trip duration (h), b) maximum distance from colony (km), c) total distance traveled (km), d) maximum trip depth (m), e–g) Home Range (HR). The (*) indicates significant differences between seasons and (**) indicates significant differences between stages



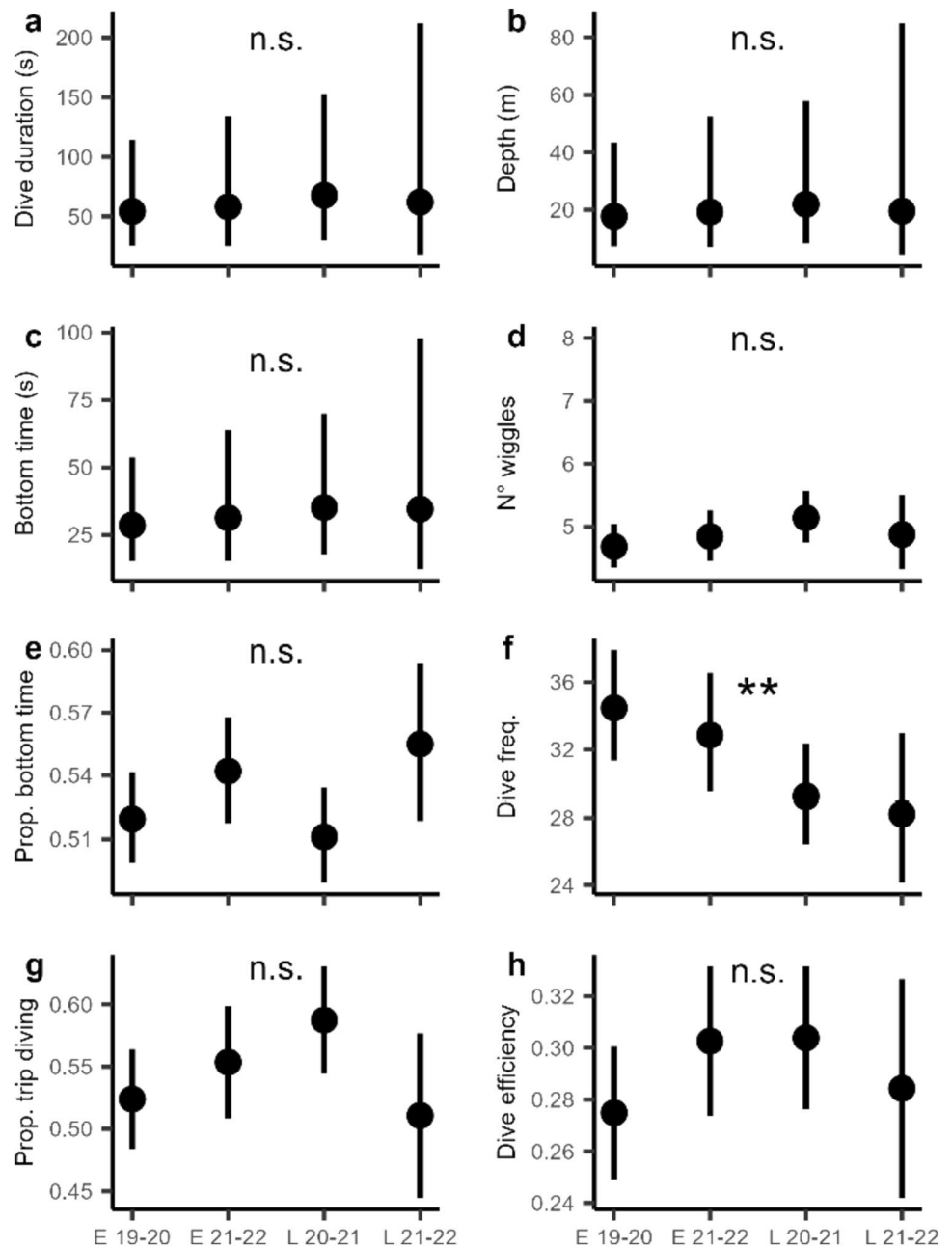
102.72 ± 2.52 s; $F = 13.71$; $p < 0.001$) and bottom time was longer (45.88 ± 1.07 s vs. 49.67 ± 1.29 s; LMM, $F = 5.11$; $p < 0.05$) than during the early guard (Fig. 6). There were also differences between seasons. During the early guard in the 2021–2022 season, dive duration (83.42 ± 2.44 s vs. 97.38 ± 2.73 s; LMM, $F = 11.9$) and time spent at the bottom lasted longer (42.29 ± 1.21 s vs. 50.35 ± 1.35 s; $F = 9.91$; $p < 0.001$), and maximum depth was deeper (72.46 ± 2.61 m vs. 86.28 ± 2.94 m; LMM, $F = 9.05$; $p < 0.001$) than at the same stage in the 2019–2020 season (Fig. 6). On the other hand, during the late guard the only variable that showed significant differences between seasons was foraging

frequency, which was higher during the 2020–2021 season (15.21 ± 0.77 vs. 11.31 ± 1.18 ; LMM, $F = 3.78$; $p < 0.05$) (Table 2, S4 and Fig. 6). The indicated values are the mean and standard error for each parameter.

Discussion

In this study, we integrated spatial location, dive, and accelerometry data from Adélie penguins rearing chicks in Ardley Island, King George Island/Isla 25 de Mayo, to characterize their foraging behavior and identify key foraging areas

Fig. 3 Diving behavior of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019–2020 and 2021–2022: E 19–20, E 21–22; late guard 2020–2021 and 2021–2022: L 20–21, L 21–22. Mean and SE (standard error) calculated from model outputs: a) dive duration (s), b) depth (m), c) bottom time (s), d) number of wiggles, e) proportion of bottom time, f) dive frequency, g) proportion of the trip diving, h) dive efficiency. The (*) indicates significant differences between seasons, (**) indicates significant differences between stages and “n.s.” indicates no significant differences



regularly used by a declining colony in an area free of sea-ice throughout the austral summer. During the chick-rearing period, both early and late guard, and across seasons, Adélie penguins breeding in Ardley Island forage in the vicinity of the colony, within Maxwell Bay. Foraging dives comprise roughly 40% of the dives penguins perform during their foraging trips, irrespective of the stage of the chick-rearing period, or the season analyzed. Our results add relevant information on Adélie penguin foraging behavior in a rapidly changing region and to the current debate on small-scale management units for the krill fishery, for which the identification of foraging areas used by predators represents critical

information to mitigate potential competition between predators and fisheries (Hinke et al. 2017; Trathan et al. 2022).

Distances covered during the trips, trips duration and area explored changed throughout the breeding season, increasing as the season progressed, with average duration of trips changing from mean values of 8.6–18.3 h in the early guard to 20.9–22.5 h in the late guard, and mean maximum distance to the colony changed from 6.6–15.2 km in the early guard to 23.8–25.2 km in the late guard. Dive frequency was higher and maximum depth was shallower during the early guard. All other dive parameters did not show any differences between stages, suggesting that trip distance and

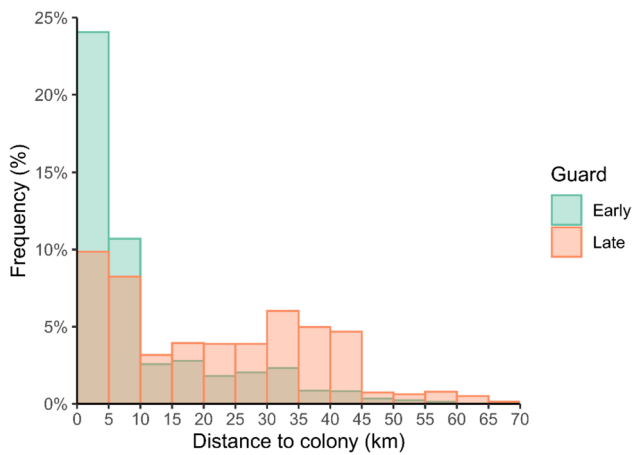


Fig. 4 Frequency distribution of distance of foraging dives to the colony (km) of Adélie penguins breeding in Ardley Island, King George Island, during early guard (green) and late guard (pink)

duration are the key parameters adjusted to account for differences in prey availability or energetic demands as the season progresses. The same was observed when seasons were compared. During the early guard in the 2019–2020 season, Adélie penguins undertook shorter trips, with maximum depth being the only other parameter where differences between seasons was observed. No significant difference was observed between late stages in any parameter. We found no differences between dive characteristics, such as dive duration, time spent at the bottom or number of wiggles, parameters often used to infer foraging effort and success (e.g., Bost et al. 2007; Riaz et al. 2020, 2023).

However, when only foraging dives were considered, we observed differences in dive characteristics, with penguins diving deeper, and dive durations and time spent at the bottom lasting longer during the late guard. We also found differences between seasons, with higher maximum dive depth and duration and time spent at the bottom lasting longer during the early guard of 2021–2022 and foraging frequency being smaller during the late guard of 2021–2022. These differences might reflect differences in prey abundance, quality and/or availability (e.g., Riaz et al. 2023), and/or penguin energetic demands as seasons progress. The use of video data in combination with GPS accelerometer tags could help validate behaviors estimates and the number of prey captured, clarifying energetic demand (Watanabe et al. 2013).

In general, the characteristics of Adélie foraging trips during chick-rearing in Ardley Island are comparable to other studies on this species in the early 90s at the same colony and other colonies in the WAP more recently, with maximum distance from the colony of less than 40 km and trip duration of less than 24 h (Wilson 2002; Oliver et al. 2013; Oosthuizen et al. 2022). When compared to other colonies around Antarctica, values of maximum distance and

trip duration in Ardley Island are lower than those reported for colonies in Adélie Land (range values from 6 to 89 km and from 16 to 96 h, Widmann et al. 2015; Michelot et al. 2021), Béchervaise Island (trip duration between 25 and 73 h, Clarke et al. 1998; Riaz et al. 2020), Prydz Bay (mean trip duration of 64 h, Watanuki et al. 1997) and in Ross Island (maximum distance values from 25 to 35 km and mean trip duration between 24 and 84 h, Ainley et al. 1998; Lescroël et al. 2010, 2020). Differences might reflect different environmental conditions between colonies, since both East Antarctica and the Ross Sea region have sea-ice cover near the colonies during the breeding season, whereas Ardley Island has no sea-ice cover at any time during the season. This would be supported by reported values of maximum distance and trip duration similar to those reported in our study, at colonies in East Antarctica during seasons with low sea ice concentration records (Ito et al. 2020; Michelot et al. 2021). Differences could also be due to colony size, given that at small colonies, like Ardley Island, individuals tend to forage closer to the colony than those in larger colonies (Ballance et al. 2009; Patterson et al. 2022). Also, note that several studies have documented that penguins, including pygoscelid, may exhibit sex-specific differences in their foraging behavior (Clarke et al. 1998; Beaulieu et al. 2010; Riaz et al. 2020). Yet, sex was only determined for some of the individuals tracked, therefore precluding statistical comparisons due to the small sample size in each season. Hence, there are some behavioral differences that may influence our results that have not been considered in this study.

During the breeding season parents must meet the increasing energetic demands of chicks by increasing foraging effort (Kato et al. 2003; Ainley et al. 2004; Clarke et al. 2006; Kokubun et al. 2010). In Nareški Point (Barton Peninsula), located 10 km away from Ardley Island, Kokubun et al. (2010) shown that, during chick rearing, both chinstrap and gentoo penguins (*Pygoscelis antarcticus* and *P. papua*) move away from the colony as the season progresses, and attributed this to a reduction in prey availability around the colony. Competition for food resources has been proposed as a regulating mechanism of pelagic seabird populations by prey depletion near the colony ('Ashmole's halo'), forcing individuals to forage further (Birt et al. 1987; Ballance et al. 2009; Patterson et al. 2022). Although the Adélie penguin colony in Ardley Island is small, many other penguins nesting on the same island and in nearby colonies may contribute to prey depletion within Maxwell Bay. The increase in foraging distance as the season progresses observed in our study might be reflecting this process.

On the other hand, the differences in foraging behavior observed between seasons might reflect inter-annual variability in krill availability. In the vicinity of our study area Salmerón et al. (2023) reported direct evidence of lower krill abundance in 2021–2022 than in 2019–2020. They showed

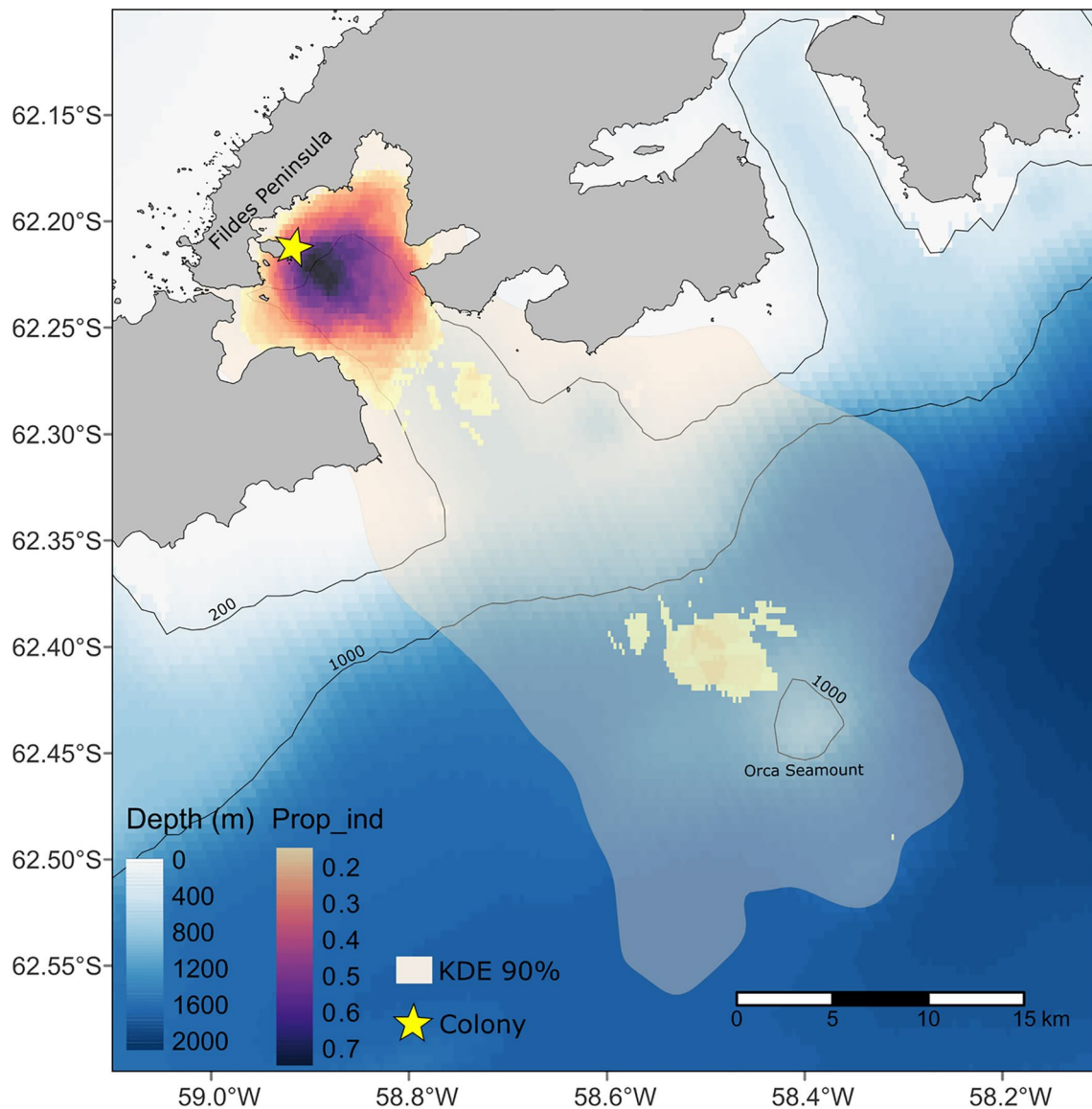


Fig. 5 Key foraging areas of Adélie penguins breeding in Ardley Island. Proportion of individuals (Prop_ind) foraging in each 0.16 km² cell is shown. Only cells where the 50% UD of at least 10% of

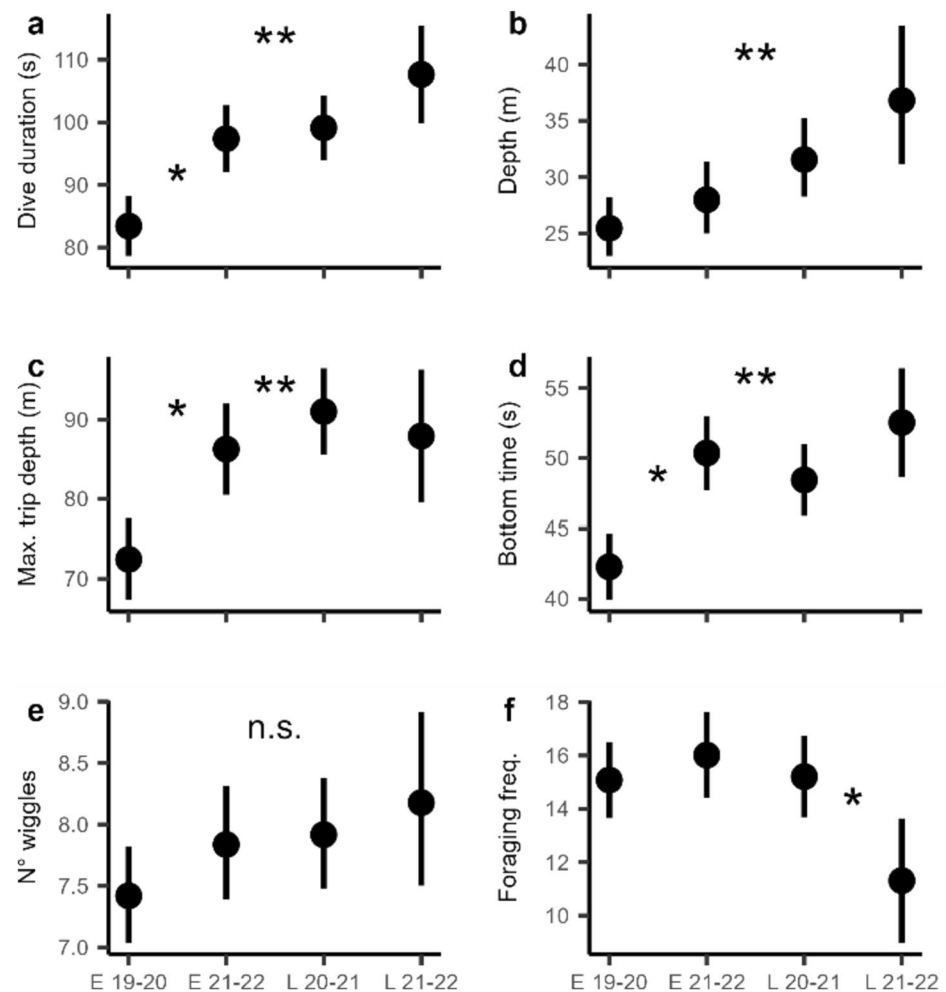
the population overlaps are shown. KDE 90% indicates the isopleth of the 90% kernel density of all locations recorded during the study

that chinstrap penguins breeding less than 20 km away from our study area, in Nelson Island, substantially increased their foraging effort during the year of low krill availability, supporting our interpretation that the differences observed in the foraging behavior of Adélie penguins in Ardley Island also reflects variations in prey availability during the study period. Our observations have also been also evidenced for Adélie penguins in different colonies around Antarctica which in response to changes in energy demand and/or prey availability/size tend to modify the distance and duration of foraging trips (Watanuki et al. 1993; Fraser and Hofmann 2003; Ainley et al. 2015; Lescroël et al. 2020), the depth of dives (Lescroël et al. 2023; Ainley et al. 2015) and/or the

type of prey (Cherel 2008; Jarman et al. 2013; Ainley et al. 2018).

Our accelerometry-data-based approach showed that the core foraging area of the colony is located within Maxwell Bay, 10 km off the colony, with this area being systematically used by more than 60% of the population throughout the seasons and across seasons. We also observed that nearly 20% of the population uses the area close to Orca Seamount for foraging (35 km from the colony), mainly during the late guard stage or during periods of low prey availability. Lee et al. (2021) report similar observations for the gentoo and chinstrap colonies breeding in Ardley Island. Both species foraged in the vicinity of the colony, within the Maxwell

Fig. 6 Characteristics of foraging dives of Adélie penguins breeding in Ardley Island, King George Island, during early and late guard between 2019 and 2022 (e.g. early guard 2019–2020 and 2021–2022: E 19–20, E 21–22; late guard 2020–2021 and 2021–2022: L 20–21, L 21–22. Mean and SE (standard error) calculated from model outputs: a) dive duration (s), b) depth (m), c) maximum trip depth (m), d) bottom time (s), e) number of wiggles, f) foraging frequency. The (*) indicates significant differences between seasons, (**) indicates significant differences between stages and “n.s.” indicates no significant differences



Bay, evidencing a clear overlap of foraging area of three species of pygoscelid penguins breeding in the island. They also reported, as did Kokubun et al. (2015), that the Orca Seamount area is a foraging hotspot used by Narębski Point's chinstrap and gentoo populations. Studies on Adélie penguins at Anver Island report similar behavior: short foraging trips (8–25 km) associated with a submarine canyon near the colony (Oliver et al. 2019; Nardelli et al. 2021). This kind of bathymetric features, such as submarine canyons and seamounts appear to increase zooplankton availability through physical processes that affect the vertical distribution of nutrients, such as upwelling, thus, constituting important areas for marine predators (Clarke et al. 2006; Santora and Reiss 2011).

Understanding the predator–prey interactions at small scales is critical for ecosystem conservation planning and resource management (Watters et al. 2020; Trathan et al. 2022). As krill catches intensify in the Western Antarctic Peninsula, particularly in coastal areas, there is an increasing need for ecological data at small spatial and temporal scales to inform potential overlap and conflicts. Although fishing in

Maxwell Bay is not currently significant, King George Island is located within one of the regions that concentrates most of the krill fishing activity (e.g., Hinke et al. 2017). Identifying relevant foraging areas in the vicinity of other penguin colonies in the northern shelf of the South Shetland Islands and Bransfield Strait, where krill fishery currently concentrates, would enable small-scale conservation measures for implementing small-scale management of the krill fishery in the region, as well as other conservation measures (e.g., Hogg et al. 2020). Here, we propose an accelerometry-data-based approach to identify these areas. Implementing conservation measures aimed at avoiding additional pressures on the main foraging areas, or the areas to which colonies resort when the availability of prey decreases, might play a key role in diminishing the potential impact of fisheries on predator populations.

Under current environmental changes in the WAP, southward contraction and krill biomass reduction trends are expected to continue, linked to positive trends in Southern Annular Mode (SAM) anomalies, which are associated with warm, windy and cloudy weather and reduced sea

ice (Atkinson et al. 2019). With reduced prey availability, changes in foraging behavior and reproductive success of penguins are expected, such as those already observed by Cimino et al. (2023) on Anver Island in years with early sea ice retreat and by Salmerón et al. (2023) associated with winter sea ice scarcity and likely deepening of the mixed layer resulting from stronger winds. Recently, it has been suggested that the coupling of climatic events and fisheries may exacerbate local effects on krill availability, affecting penguin breeding populations (Watters et al. 2020; Krüger et al. 2021). Thus, in the WAP, identifying local foraging hotspots for krill-dependent predators, might be crucial for determining areas of ecological importance that require consideration in management measures.

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Author contribution ALM-G, AK, MC, YR-C, AB and AS contributed to the study conception and design. ALM-G, AB and AS performed data collection. Data analysis was performed by ALM-G, AK, MC, NG and AS. The first draft of the manuscript was written by ALM-G and AS, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval All penguin handling procedures were reviewed and approved by the Honorary Commission of Animal Experimentation of Uruguay (CHEA protocol N° 1312).

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