DOES FORAGING SUCCESS PREDICT SUBSEQUENT FORAGING BEHAVIOR IN PYGOSCELIS PENGUINS?

by

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My lab mates, friends, and family for without which I could never have completed this work

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ABSTRACT

In a patchy prey environment, optimal foraging theory predicts that central place foragers will discretize horizontal movement and vertical movements into directed and resident foraging behaviors and that high foraging success should lead to similar sequential foraging trips. Here we use high resolution GPS and depth records to track the foraging locations and estimate forage success of two *Pygoscelis* penguin species in a known biological hotspot to test the predictions of optimal foraging theory. Over two breeding seasons, we tagged 71 penguins near Palmer Station in the West Antarctic Peninsula. We estimated foraging activity from the complexity of depth records and linked them to horizontal patterns of resident and directed movements measured by GPS tags. Contrary to theoretical expectations, we found that there was no relationship between movement modes and foraging rate. We also found that the degree of similarity between sequential trips was not predicted by foraging success, wind speed, or tidal stage. Sequential foraging trips were also not significantly more similar to each other than other non-sequential foraging trips. Our overall findings suggest that the penguins in this region forage during both directed and residential movements, which is not expected if they were following optimal foraging theory. The horizontal patterns of resident and directed movements were not good predictors of foraging activity. We suggest that the abundance and reliability of prey in the local region may explain why these penguin colonies do not follow the expectations of optimal foraging theory.

Chapter 1

INTRODUCTION

Predator foraging behavior plays a critical role in their population and community dynamics, influencing distribution and size, breeding success, and predator-prey interactions (Sutherland 1996, Kokko & Lopez-Sepulchre 2006). Therefore, understanding predator foraging strategies is important for conservation efforts and the field of movement ecology. Seabirds are sentinels for ecosystem health (Cairns 1987, Reid et al. 2005, Piatt et al. 2007) and are central place foragers during their breeding season, having a nest from which they leave and return to when collecting prey. During foraging trips, they must locate prey within a dynamic environment while managing energetic demand and avoiding predators (Kooyman & Ponganis 1998, Ainley & Ballard 2012). The mix of biotic and abiotic limitations on foraging behavior potentially make foraging decisions by seabirds complex.

Optimum Foraging Theory (OFT) assumes that foragers will maximize time or effort in locations where they can acquire the most energy and minimize the cost to gain that energy (Pyke 1984), and serves as a theoretical framework to evaluate observed foraging behavior. One of the most he most prominent patterns observed in foragers is Area Restricted Search (ARS). ARS is a foraging model where foragers seek out and target areas of high prey density (Kareiva & Odell 1987). This results in the animal switching between “directed” and “resident” modes in their observed foraging tracks. Resident modes are characterized by tortuous movement and are assumed to be associated within a high density of resources, such as a prey patch.

Directed modes are those between tortuous bouts and are generally faster and straighter. According to the ARS behavioral model, most foraging is occurring during resident behavior and little foraging is occurring during directed behaviors.

Central place foraging predators must balance the energy expended to leave and return to their central place with the energy gained through foraging. According to OFT, if prey is dispersed in patches of differing quality, predators will travel to either one or multiple patches of high quality prey and leave that patch when satiated or when the patch quality falls to below an optimum level (Orians & Pearson 1979). Recently, new findings in aquatic systems are beginning to show that air-breathing marine foragers do not always align with OFT tenets. For example, Watanbe et al 2014 found that penguins in the Ross Sea do not significantly decrease patch quality before moving onto another patch, a direct conflict with OFT. Additionally, Riaz et al. 2021 found that Adélie penguins at Béchervaise Island had decreased foraging activity during periods of resident movement and concluded that these movement types were indicative of resting behavior. However, in this study, periods when the tags were dry were not removed from the analysis. This could have confounded findings of more intense foraging behavior. Therefore, the possibility of high foraging during resident movement types could remain if haul out behavior is accounted for using wet-dry sensors. Understanding where and how these organisms forage and the degree to which they are bound to OFT principles is vital to proper conservation and management of these species.

An inherent assumption within OFT is that predators have some knowledge or memory of the distribution and energy availability of prey within their foraging region. Theoretically, with some information of prey patch locations the predator would weigh the costs and benefits of moving to different patches of prey and deciding when to end a foraging trip. The scales at which this knowledge is acquired is difficult to test, especially within an ecosystem with shifting prey distributions. Knowledge of prey distributions has been investigated across breeding seasons (Ford et al 2015), but whether predators can integrate prey distribution knowledge at a day-to-day scale is not known. Bonadonna et al 2001 found that fur seals were more likely to return to the same foraging locations during sequential trips, and the authors theorized this was due to the success of the previous outing. However, this study only examined horizontal positional data from satellite tracks and could not confirm the level of foraging that occurred. If a predator were to have a highly successful foraging trip, it could be beneficial to remember the foraging locations of that trip and return on the next foraging trip. It is possible a predator could significantly decrease the amount of prey within that foraging patch, therefore it would be beneficial to search elsewhere. We do not yet know if certain predators have the mental capacity to remember specific foraging locations and tie them to success at this small of scale.

The development of telemetry and bio-logging technologies has greatly increased our ability to resolve marine animal movements. Satellite based telemetry tags have been widely used to identify essential foraging and breeding habitats, and migratory pathways of multiple marine taxa (Block et al. 2011). Recent developments of GPS based tags have increased the accuracy of recorded animal relocations and allowed for a finer scale examination of predator decision making. Time depth recorders (TDRs) give an accounting of the number and shape of dives performed by a marine predator and are useful in identifying probable prey capture events. The difficulty in recording long term ground-truthed accounts of foraging, such as through video or esophageal temperature recorders (Yoshino et al. 2020, Ropert-Coudert et al. 2001, has resulted in the proliferation of studies that use either telemetry tags or TDRs to infer different foraging behaviors. Studies that have examined foraging in both horizontal and vertical, have varied in the degree at which OFT tenets are followed (Bestley et al. 2015, Ramasco et al. 2015, Riaz et al. 2021). Additionally, modelling analyses have increased in complexity, with state space models (SSMs) becoming widely used. SSMs use a behavioral switching framework where the movements are categorized into discrete transit and foraging states. Movement can also be modeled continuously with time-varying movement persistence models.

On Anvers Island, Antarctica near Palmer Deep Canyon, high biomass of Antarctic krill (*Euphausia superba*) and other zooplankton supports multiple colonies of both Adélie penguins (*Pygoscelis adeliae*) and gentoo penguins (*Pygoscelis papua*). Evidence suggests that a recirculating feature over Palmer Deep could retain krill in the region, thus supporting a predictable prey source for predators (Hudson et al. 2019, 2022). During the austral summer, in conjunction with the penguin breeding season, water flows along isobaths into the canyon creating a subsurface cyclonic eddy that has an approximate diameter of 50 km and is mainly contained beneath the mixed layer depth (Hudson et al. 2021). This feature retains a particle layer of detrital materials with residence times within the eddy being as high as 175 days. The presence of this feature could enhance microbial activity, be a direct source of food for keystone zooplankton in the regions, actively retain the zooplankton themselves, or some combination of these. In a simulated study, the deep recirculating eddy was shown to enhance the delivery of diurnal vertical migrating krill to nearby penguin foraging regions on Anvers Island (Hudson et al. *in press*). Regardless of the direct function of the canyon on biological activity, krill aggregations of varying sizes and densities are known to occur which results in a potentially complex, but abundant, prey field (Bernard et al. 2017). Both of these predators have been shown to preferentially associate with small scale physical aggregating features within this region (Oliver et al. 2019), however how they find and identify these areas is not known.

The objective of this study is to investigate the applicability of OFT tenets on Adélie and gentoo penguins in a known biological hotspot near Palmer Station, Antarctica. This study was conducted over two breeding seasons during the chick rearing phase when the energy demand on these species is high. We examine the sequential foraging trips for evidence of short-term memory of foraging success and examined possible environmental predictors of trip similarity. Additionally, we fit movement persistence models to trips to determine whether foraging predicted by horizontal measures is matched by foraging predicted from depth records. We hypothesized that 1) increased foraging success, determined by dive behavior, would result in similar sequential trips, and 2) that horizontal movement modes of residency, as opposed to transit, of will align with increased foraging activity.

Chapter 2

METHODS

This study was conducted during two austral summers, at Adélie penguin colonies located at Humble Island (64°45’S, 64°05’W), Torgersen Island (64°46’S, 64°04’W), and Biscoe Point (64°48’S, 63°46’W), and at the gentoo penguin colony located at Biscoe Point (Figure 1). These specific sites were chosen because they are part of a long term study conducted with the Palmer Long-Term Ecosystem Research (PAL LTER) long-term monitoring project.

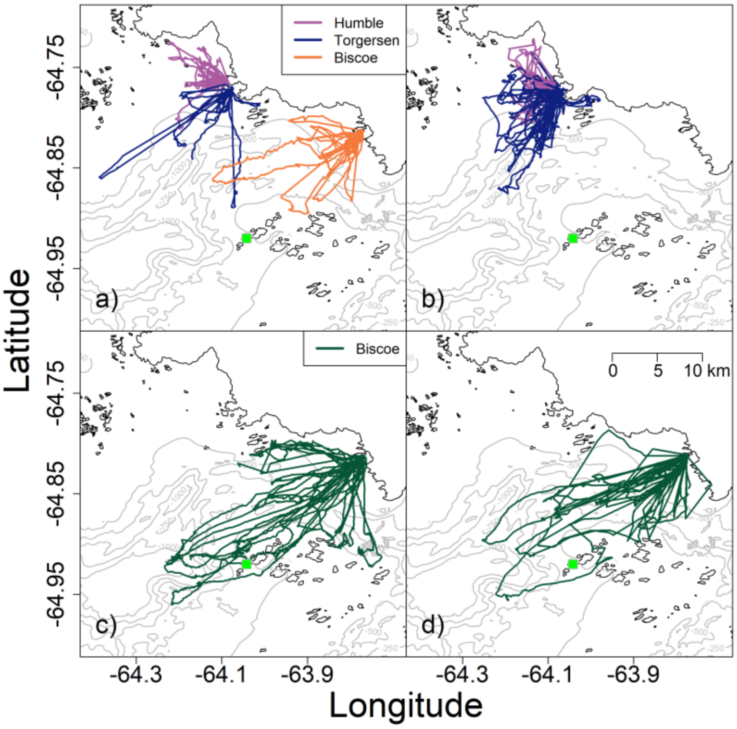

Figure 1 Map of trips included in the Fréchet and sum distance calculations. Color of trip indicates colony of origin. Green square indicates location of Wauwerman Island weather station. A) Adélie penguins from 2019-2020 season, b) Adélie penguins from 2020-2021 season, c) gentoo penguins from 2019-2020 season, d) gentoo penguins from 2020-2021 season.

In this study, Adélie and gentoo penguins were double tagged with fast-loc GPS tags and a time-depth recorder (TDR) measuring pressure at 0.5 Hz while wet (Lotek LAT1400, Lotek Wireless, Inc, St. John's Canada). Tags were adhered to the anterior feathers on the lower dorsal area of the penguin using waterproof tape and plastic zip ties. All protocols were carried out in accordance with the approved guidelines of the Columbia University (Assurance #AAAS2504) and University of California Santa Cruz (Proposal Code: Cimim2204dn) Institutional Animal Care and Use Committee for the 2019-2020 and 2020-2021 seasons respectively (Appendix B). Tags were deployed on individuals for 1-7 days before being removed and reattached to another penguin. We tagged 48 Adélies and 23 gentoos over the course of the 2019-2020 and 2020-2021 austral summers (Table 1). Drift in the depth data for tags was zero offset corrected using the *calibrateDepth* function in the R package diveMove (Luque 2007). Drift was not corrected for 7 deployments, as on 6 of these deployments (all Adélies, 5 Humble Island, 1 Torgersen Island) depth recordings shallower than 1 meter were not taken, and on 1 deployment (1 Adélie, Humble Island) depth recordings shallower than 5 meters were not taken. GPS data were filtered for erroneous locations based improbable swimming speeds (>2.8 m s^{-1}).

Table 1 Number of Adelie and gentoo penguins tagged by colony and season.

	2019-2020		**2020-2021**	
	Penguins Tagged	**Trips Recorded**	**Penguins Tagged**	**Trips Recorded**
Adelie - Humble Island	12	23	4	14
Adelie - Torgersen Island	13	24	13	45
Adelie - Biscoe Point	5	13	1	1
Gentoo - Biscoe Point	14	32	9	26

GPS location and TDR depth data were time matched and dives were identified using the *diveStats* function in diveMove (Luque 2007). Dive behaviors were categorized into transit, search, or forage based on Cimino et al. 2016. Briefly, a transit dive is a short dive with a maximum depth shallower than 4 meters or duration of less than 20 seconds. Forage dives are dives that included bottom time, plateaus, or two or more wiggles. Bottom time is the duration of the dive spent within 85% of the maximum depth of the dive. The 85% of maximum depth is known as the ledge. If more than 25% of the dive occurred under the ledge, it was classified as a forage dive. A plateau is a portion of the dive that is relatively flat over time and occurs in depths shallower than the ledge. This is defined as a portion of the dive having variation in depth shallower than 10% of the maximum depth over a time greater than 25% of the dive duration. Wiggles are undulations that signify pursuit of prey and were defined as a deviation in depth of greater than 2 meters. If two or more wiggles occurred, the dive was classified as a forage dive. If a dive was longer than 90 seconds, we also defined it as a forage dive as it was an indication of more intense foraging effort. If the dive fell outside of the criteria of both transit (i.e. the dive was greater than 4 meters and longer than 20 seconds) but did not reach the criteria for being classified as a forage dive (presence of bottom time, a plateau, or 2 or more wiggles), it was classified as a search dive.

Forage trips were visually inspected and defined as sections with both full GPS and dive data from when an individual left and returned to their colony. GPS locations on land were removed. A total of 178 individual forage trips were recorded over both years and both species (Figure 1). To define foraging trip success, we used three metrics: dive frequency, total wiggles, and vertical dive effort. Dive frequency in the number of forage dives divided by the total trip duration, total wiggles is the total number of wiggles found during the trip, and vertical dive effort is the sum of maximum depths of forage and search dives divided by the trip duration (Riaz et al. 2020).

To compare the similarity of sequential trip trajectories, a metric known as the Fréchet distance (Alt & Godau 1995) was used from the R package *SimilarityMeasures* (Toohey 2015). The common analogy is a person walking their dog with an extendible leash. As the person and their dog move independently, the leash changes length while connecting them. The Fréchet distance is the maximum length of the leash as the person and their dog move along their respective tracks (Figure 2).

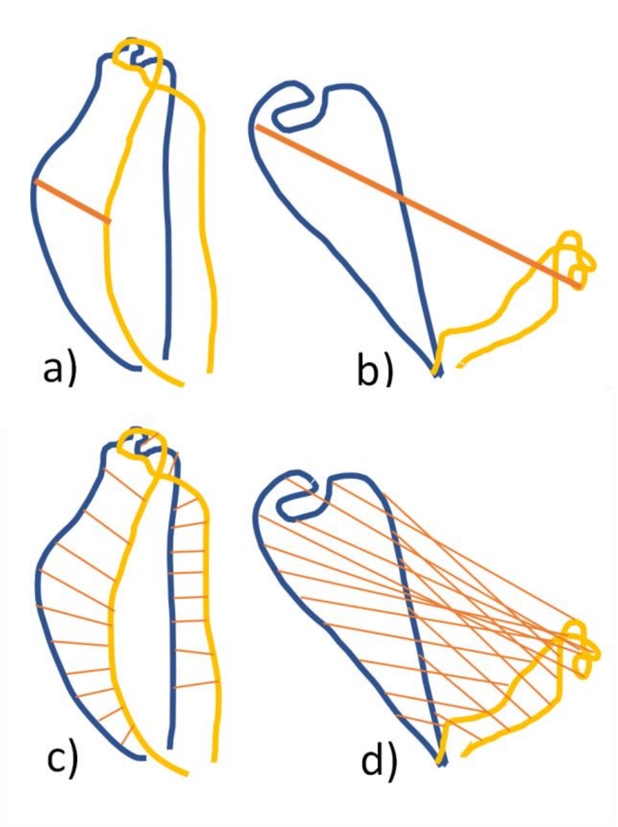

Figure 2 An illustrative example of how Fréchet distance (a,b) and sum distance (c,d) were calculated on two sequential trips. A) and c) show two very similar trips while b) and d) show two very dissimilar trips.

We chose this measure because it does not require that the trajectories have the same length, and is good at distinguishing trips that travel to different foraging locations (Cleasby et al. 2019). Additionally, as the Fréchet distance is a nonparametric measure of distance (maximum), we created a complimentary measure to quantify trips that are not based on estimates of maximums in which we paired 100 points equally spaced along each trip and measured the distance between them, then summed these distances. We refer to this as ‘sum distance’. As these analyses measure the difference between sequential trajectories, only tags that recorded multiple trips from an individual were included. For example, if a tag recorded three full foraging trips, we could conduct 2 comparisons, between the first and second and second and third trips. From 178 total trips, 156 trips were included in the similarity analysis resulting in 112 comparisons. Daily average wind speed and tidal data were collected by the Antarctic Meteorological Research Center at a weather station near Palmer Station (Figure 3). Wind speed was averaged over the day from the Wauwerman Islands weather station. Tidal stage was also assigned to each trip based on which stage occurred for the majority of the trip.

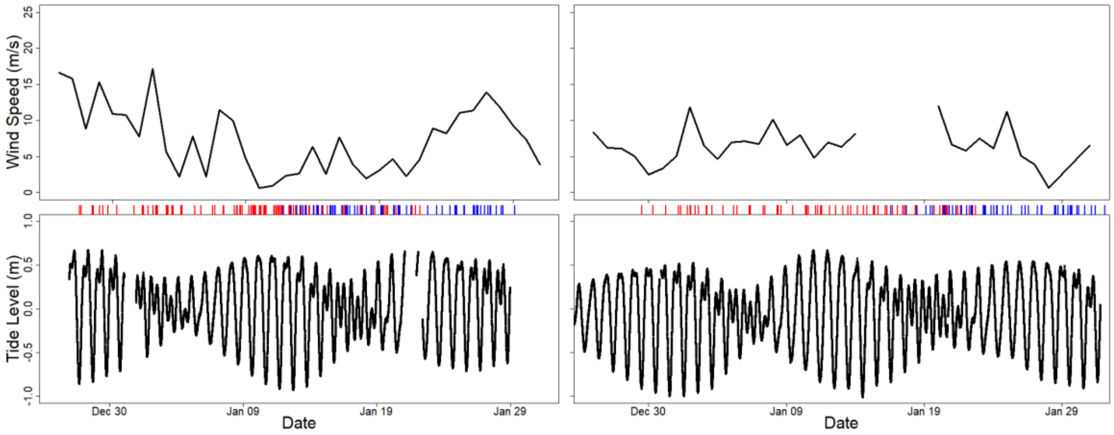

Figure 3 Wind and tide data collected for the foraging region near Palmer Station, Antarctica. Winds were daily averaged from the Wauwerman weather station and tide level was collected from the tidal gauge outside Palmer Station. The start of Adélie (red) and gentoo (blue) forage trips are indicated above the tidal data. A) Daily averaged wind speed during the 2019-2020 season, b) daily averaged wind speed during the 2020-2021 season, c) tide level during the 2019-2020 season, d) tide level during the 2020-2021 season.

To test our hypothesis that increased forage success resulted in decreased Fréchet and sum distances, we calculated linear mixed effect regressions for each species with dive frequency, total wiggles, vertical dive effort, season, colony, average daily wind speed of the first day, averaged daily wind speed of the second day, absolute difference in average wind speeds from the first and second day, tidal stage of the first trip, and tidal stage of the second trip as explanatory variables and separately Fréchet distance and sum distance as predictor variables. Individual was set as the random effect. Additionally, the wind gauge at the Wauwerman Island weather station was undergoing repairs from January 13 - 19th of 2021, no wind data is available for the trips that occurred during those days (n ADPE trips = 13, n GEPE trips = 2). Therefore, we ran a model including wind parameters on all comparisons where wind data was present and another model on all comparisons collected and excluded the wind parameters.

To test the if the distribution of Fréchet distances and sum distances from observed sequential trips were different from non-sequential trips, we created null model comparisons by randomly shuffling observed trip, thus pairing foraging trips with other, non-sequential trips from the same colony and species. We chose to shuffle existing trips to have the most accurate measure of how real penguins move, and did not want to bias our results by trying to simulate their movement and foraging locations. This consisted of 250 sets of 78 Adélie and 34 gentoo Fréchet and sum comparisons (28000 comparisons total). For each set, the same number of comparisons from each species and colony are included as in our real set of sequential trips (34 gentoo Biscoe Point comparisons, 9 Adélie Biscoe Point comparisons, 24 Adélie Humble Island comparisons and 45 Torgersen Island comparison). The two trips were randomly selected with replacement from the same species and from the same colony, and the Fréchet and sum distances between the two trips were calculated. If two trips chosen for similarity analysis were sequential trips from the same individual, they were rechosen. Seasons were not separated to give a larger pool of trips to sample from. We performed Kolmogorov-Smirnov tests on the Fréchet distances and sum distances from each shuffled set to the corresponding set of Fréchet and sum distances from unshuffled trips. We chose to measure the KS tests at the $\alpha = 0.01$ and we also applied a Bonferroni correction (0.01/250) to account for multiple tests ($\alpha = 4 \times 10^{-5}$).

To split trips into sections of “directed” and “resident” movement, we fitted a continuous-time correlated random walk State Space Model (SSM) to the trips with at least 25 GPS positions (n = 143) using the “*fit_ssm*” function in the R package *foieGras* (Jonsen & Patterson 2021 foieGras Package, Jonsen et al. 2020). Then, we fit a time varying movement persistence model (γ_t) to the fitted location estimates using the *“fit_mpm”* function from “*foieGras*”. Movement persistence measures the autocorrelation in a track’s speed and direction and returns the persistence parameter (γ_t) on a continuous scale of 0 (low movement persistence indicating resident movement) to 1 (high movement persistence indicating directed movement) (Figure 4) (Jonsen et al. 2019). Values of γ_t closer to 1 indicate faster, straighter, and more directed movements, while γ_t values closer to 0 indicate slower, resident movements with larger turning angles between relocations. We chose a cutoff of 0.75 to differentiate between “directed” and “resident” movement types (Jonsen et al 2019, Riaz et al 2021). Portions of these sections where the animal is out of the water were removed from the analysis. During each “directed” and “resident” section of a trip, we calculated the forage and search dive frequency, total wiggles hr^{-1}, and vertical dive effort to assess foraging effort. Sections lasting less than 5 minutes were removed to not artificially bias areas with zero foraging effort. Foraging effort metrics were compared within species using a Wilcoxon rank sum test at the $\alpha = 0.01$ level.

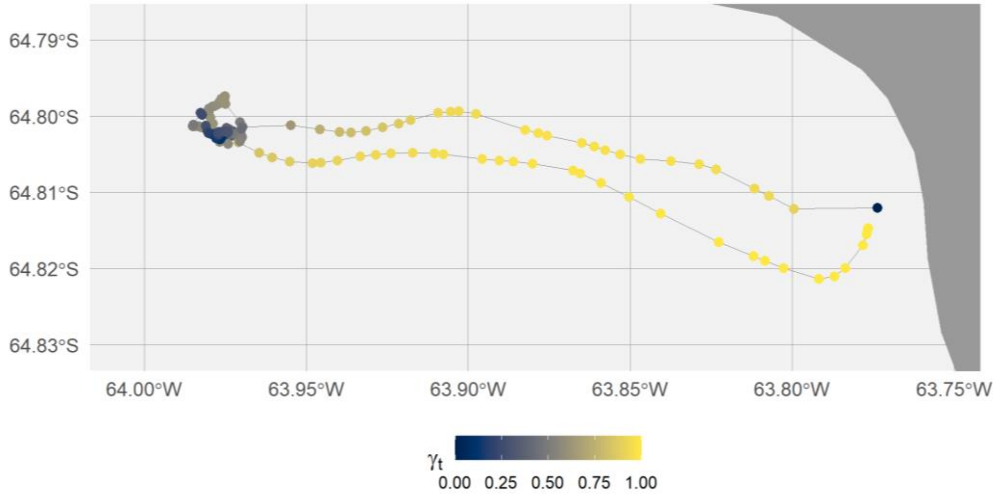

Figure 4 An example of the movement persistence model fitted to an individual gentoo penguin trip. High gamma values near 1 (bright yellow) indicate sections of directed transit behavior, while low gamma values (darker blue) indicate sections of tortuous resident movement.

Chapter 3

RESULTS

We recorded 92 foraging trips from the 2019-2020 season and 86 foraging trips from the 2020-2021 season that had both GPS location and TDR depth data for the entirety of the trip. In the 2019-2020 season, we recorded 60 Adélie foraging trips (23 from Humble Island, 24 from Torgersen Island, and 13 from Biscoe Point), and 32 gentoo foraging trips (all from Biscoe Point). In the 2020-2021 season, we recorded 60 Adélie foraging trips (14 from Humble Island, 45 from Torgersen Island, 1 from Biscoe Point) and 26 gentoo foraging trips (all from Biscoe Point) (Table 1). Adélie penguins on average travelled closer to their colonies and for shorter durations than gentoos penguins (Table 2).

Table 2 Trip level statistics for full foraging trips by Adélie and gentoo penguins averaged over colony and year. Mean, confidence intervals, and ranges are listed.

	ADPE mean (CI)	**ADPE range**	**GEPE mean**	**GEPE range**
Maximum Dist from Colony (km)	5.03 (4.42-5.63)	0.41 – 17.68	12.69 (10.91-14.47)	1.18-27.41
Duration (hr)	5.07 (4.45-5.70)	0.19-20.40	9.70 (8.67-10.72)	2.72-22.64
Dive Freq (dives hr^{-1})	24.28 (22.75-25.80)	2.47-50.67	15.78 (14.59-16.98)	0.89-30.36
# Wiggles	20.68 (17.38-23.98)	0-115	35.39 (29.75-41.04)	0-145
Vertical Dive Rate (m hr^{-1})	324.1 (298.5-349.7	11.9-859.3	595.4 (539.5-651.3)	6.3-1095.7
Fréchet Distance (km)	4.07 (3.39-4.76)	0.48-15.15	7.49 (5.84-9.14)	0.92-22.05
γ_t	0.742 (0.706-0.778)	0.212-1	0.831 (0.796-0.866)	0.191-0.959
Proportion directed movement	0.479 (0.416-0.541)	0-1	0.647 (0.568-0.726)	0-1
Proportion resident movement	0.320 (0.262-0.378)	0-0.944	0.174 (0.125-0.223)	0-0.617

We recorded 14,645 Adélie forage dives over both seasons, 12,961 of which occurred in conjunction with location data and 15,129 gentoo forage dives, 9,582 of which occurred in conjunction with location data. Adélie penguins had shallower and short average dives than gentoos, however the average amount of wiggles in dives was similar (Table 3). When calculating foraging success across all full foraging trips, Adélie penguins had a higher dive frequency than gentoos, but less total wiggles and a lower vertical dive rate (Table 1).

Table 3 Dive statistics from Adélie and gentoo penguins split by season. Number of dives are listed and statistics listed are means with confidence intervals in parentheses.

	Adelie		**Gentoo**	
	2019-2020	**2020-2021**	**2019-2020**	**2020-2021**
Forage Dives	7835	6810	8485	6644
Forage Dives with Locations	6702	6259	6019	3563
Search Dives	1632	1636	788	807
Search Dives with Locations	1430	1571	578	424
Average Max Depth (m)	14.91 (14.61-14.22)	14.80 (14.59-15.01)	39.57 (38.92-40.23)	39.08 (38.37-39.78)
Average Dive Duration (sec)	69.9 (58.2-81.6)	60.8 (60.0-61.5)	96.6 (95.4-97.9)	111.8 (109.7-113.9)
Average Bottom Time (sec)	20.8 (20.6-21.0)	21.7 (21.5-21.9)	31.6 (31.2-31.9)	37.5 (36.9-38.1)
Average Wiggles	0.21 (0.19-0.22)	0.19 (0.18-0.21)	0.22 (0.21-0.24)	0.37 (0.35-0.39)

A total 31 Adélie and 13 gentoo individuals recorded at least 2 foraging trips from both seasons. There were 109 Adélie trips and 47 gentoos trips were included in our sequential trip analysis resulting in 78 Adélie repeated trip comparisons and 34 gentoo repeated trip comparisons. Gentoo trips had larger Fréchet distances than Adélie trips, however this is most likely due to the wider range of gentoo foraging trips (Table 1). There was no clear relationship between Fréchet and sum distances and any of our three foraging success metrics in either species (Figure 5). Additionally, average wind speed for either day and absolute difference between the days had no explanatory power (Figure 6). Only one of the mixed effect models that we calculated saw significant fixed effects at the $\alpha = 0.01$ level. In the Adelie sum distance model where wind data was excluded, Humble Island penguins had significantly lower sum distances (Estimate = -200555.52, Std. Error = 66071.57, t = -3.035, p = 0.00581). These penguins foraged very close to their island of origin and almost exclusively in Wylie Bay. Additionally, total wiggles in this model had a weak positive effect on the sum distance (Estimate = 3338.19, Std. Error = 1246.59, t = 2.678, p = 0.00850). (Appendix A, Tables 4-11). Two of our foraging metrics (Dive Frequency and Vertical Dive Effort) showed no significant explanatory power in any model and Total Wiggles showed weak effect (56 m) in the opposite direction of our expectation in only one out of eight models.

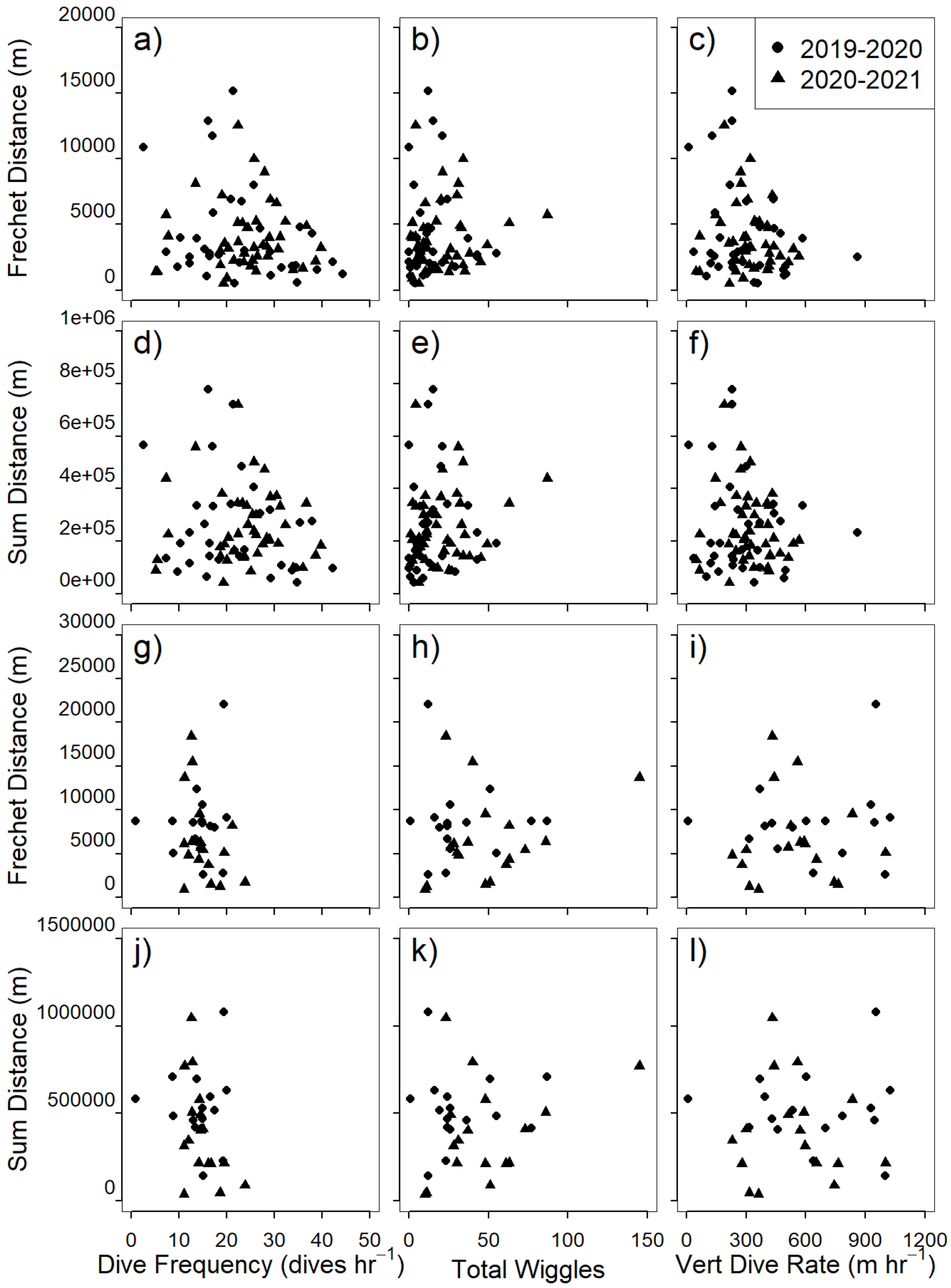

Figure 5 Scatter plots of similarity metrics against forage success metrics for Adélie (a-f) and gentoo (g-l). Shape indicates season. No significant relationships were found between and of the similarity metrics and any of the success metrics in either species.

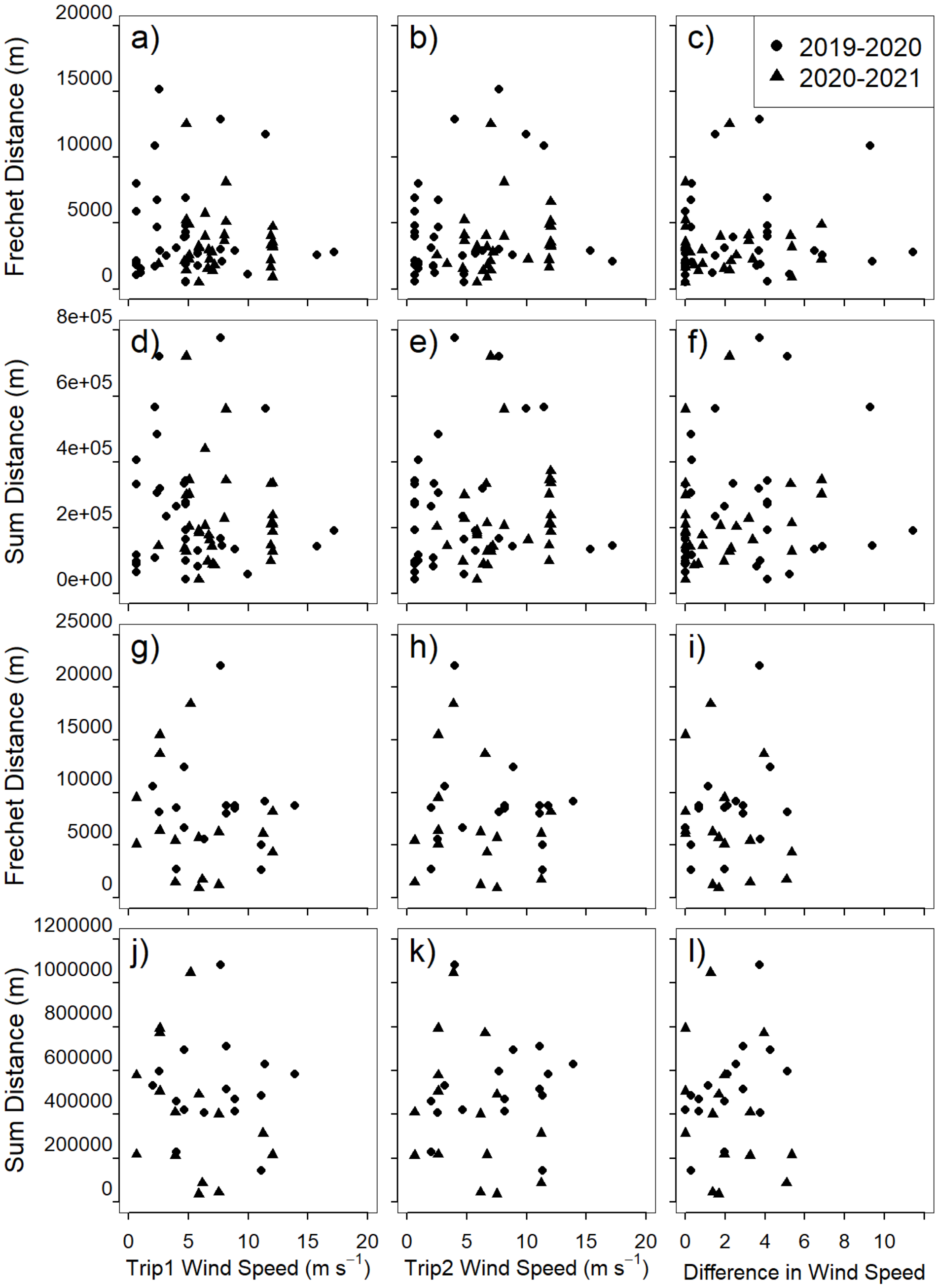

Figure 6 Scatter plots of similarity metrics against averaged daily wind speed for the first day, the sequential day, and absolute difference between wind speed between the two days. for Adélie (a-f) and gentoo (g-l). Shape indicates season. No significant relationships were found between and of the similarity metrics and any of the wind metrics in either species.

We produced species specific null models to test whether the distribution of the Fréchet and sum distances we measured differed from non-sequential trips (Figure 7). We tested these distributions at an α level of 0.01 and also applied a Bonferroni correction ($\alpha = 4x10^{-5}$) to account for multiple comparison tests. For Adélie penguins, 211 out of 250 KS tests concluded the distribution of Fréchet distances was significantly different from unshuffled trips at the 0.01 level and 16 were significantly different at the $4x10^{-5}$ level. 48 out of 250 sum distance distributions were significantly different at the 0.01 level and 0 was different at the $4x10^{-5}$ level. For gentoos, 121 out of 250 KS tests concluded the distribution of unshuffled Fréchet distances was significantly different at the 0.01 level and 7 were significantly different at the $4x10^{-5}$ level. 38 out of 250 sum distance distributions were different at the 0.01 level and 0 were different at the $4x10^{-5}$ level.

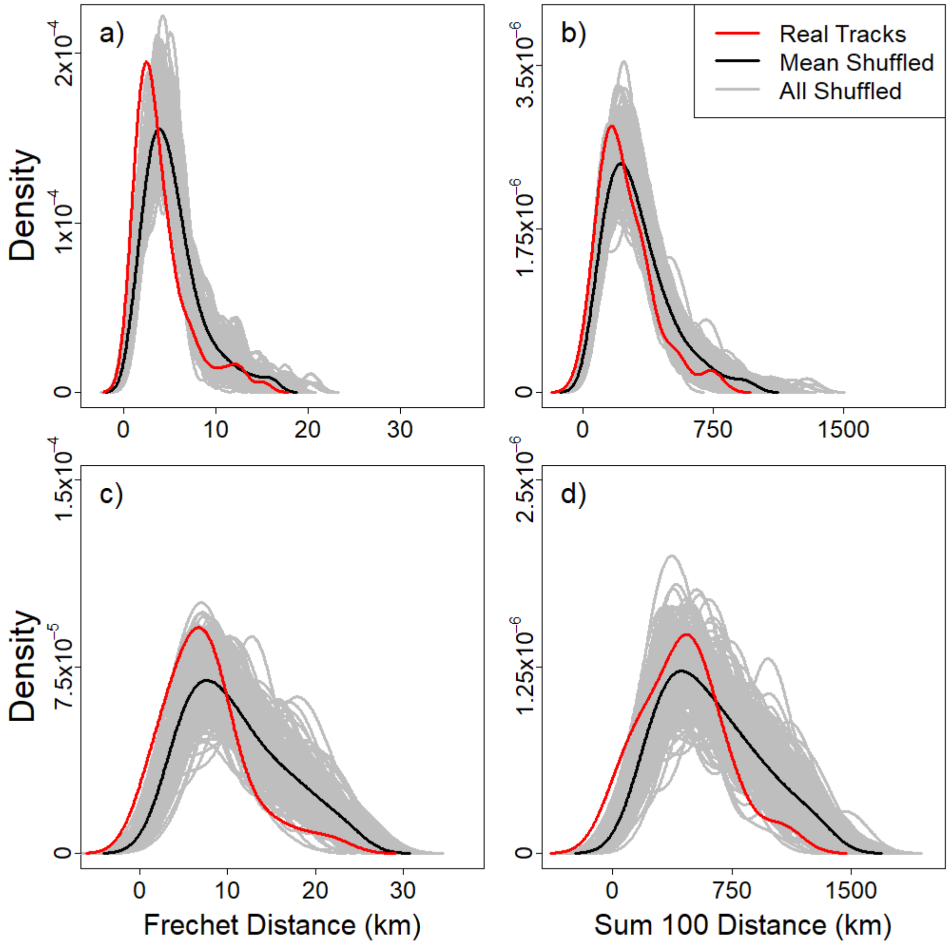

Figure 7 Density plots of sets of shuffled trips. Gray lines are the density of all 250 sets of shuffled trips. The black line is the mean of the shuffled sets and the red line is the density of similarity metrics from the real, unshuffled trips. All real, unshuffled densities are shifted slightly left from our null model analyses. Note the differences in each y axis. A) Adélie Fréchet distances, b) Adélie sum distances, c) gentoo Fréchet distances, d) gentoo sum distances.

Both Adélies and gentoos spent a higher proportion of time during foraging trips in directed movement than in tortuous movement (Table 1). There were 366 directed sections and 279 resident sections across species and years when calculated using fitted values. For sections calculated from movement persistence model, there was no significant difference in dive rate, wiggles hr^{-1}, or vertical dive effort between directed and resident sections in either species at the $\alpha = 0.01$ level (Figure 8).

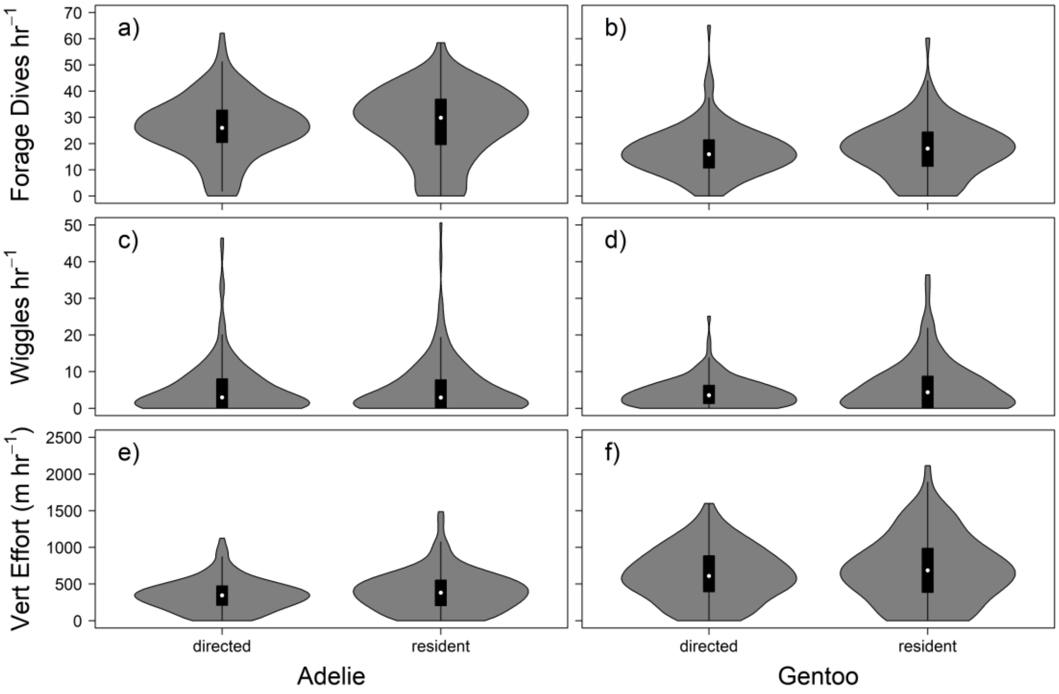

Figure 8 Violin plots of foraging effort during sections of directed and resident movement modes for each species. No significant difference in foraging effort between movement modes was found in either species in dive frequency, wiggles per hour, vertical dive effort in either species at the $\alpha = 0.01$ level. A) Adélie forage dive rate, b) gentoo forage dive rate, c) Adélie total wiggle rate, d) gentoo total wiggle rate, e) Adélie vertical effort, f) gentoo vertical effort.

Chapter 4

DISCUSSION

We used high resolution telemetry, diving behavior, and environmental data to test the applicability of two tenets of the Optimum Foraging Theory (OFT) model to two central place foraging seabirds. Under OFT, predators are expected to integrate prey capture success into subsequent foraging trips and to focus foraging efforts in discrete resident modes of movement. Our results suggest that that that previous forage success has no detectible impact on subsequent foraging trip similarity. While distribution of Fréchet and sum distances was lower than those produced by our null models, there was no relationship between environmental factors such as tidal stage or average wind speed and Fréchet or sum distances. There were no differences in effort allocation rates between directed and resident movement segments, suggesting that interpreting directed horizontal behaviors (transiting) as modes that lack foraging may be inappropriate.

We found no evidence that forage success from the previous trip predicted similarity to the next foraging trip in either Adélie or gentoo penguins. Dive rate and vertical dive rate showed no relationship with either Fréchet or sum distances, while total wiggles only showed a weak positive relationship in one of our eight models. Similarly, we found no relationship with first trip wind speed, sequential trip wind speed, or absolute difference between first and sequential trip wind speed. The lack of memory apparent in the penguins' foraging behavior could mean that they do not possess the mental capacity to remember the fine-scale locations of high quality prey patches. This assumes that (1) penguins are mainly foraging at high density prey patches, (2) these prey patches do not shift on day-to-day scales, and (3) are abundant enough throughout the region that penguins can afford to forget them on their next foraging trip and find other patches. Lack of evidence for memory use could also point to the diffusivity or unpredictability of prey within these predators' foraging range. If the penguins are not returning to previous foraging locations when success is high, this could mean that they know that prey may have shifted away from that location and therefore it would confer little benefit to return. These scenarios posit two different distributions of krill surrounding these penguin colonies. Either, high density patches of prey are so abundant that memory is not necessary for successful foraging, or there exists enough krill in low densities that penguins can sustain themselves on while searching for unpredictable high density patches.

Our attempts to discern whether the distribution of Fréchet and sum distances differed from non-sequential trips were mixed, however distance type and p value used had a large impact. When the Bonferroni correction was applied, our KS tests determined that the majority or all of shuffled distributions were drawn from the same distribution as our real unshuffled trips. From the Fréchet KS tests, we cannot fully reject the possibility of nonrandom sampling by the penguins. However, our sum distance KS tests showed strong evidence that the unshuffled trips did not differ from random. We can conclude from this that if there is some factor that impacts sequential trip similarity, the effect is very weak. This could be environmental parameters that we did not measure and that exist at this specific scale that the penguins are effectively selecting (although not necessarily cognitively selecting). One such parameter, Lagrangian Coherent Structures (LCSs), are dynamic converging features, such as eddies, jets, and fronts, that exist at meso to sub-mesoscales. LCSs aggregate neutrally buoyant particles and are associated with higher zooplankton density (Harrison et al.

2013) and seabird foraging activity (Nel et al. 2001, Hyrenbach et al. 2006). Previous work in this area using ARGOS satellite tags has shown that both species of penguin preferential select aggregating LCSs for foraging (Oliver et al. 2019). The factor driving the possible weak selection could be a day-to-day shifting of LCSs that the penguins are attracted to. Further studies in the tracking and understanding of LCSs and the affect they have on trip similarity should be conducted.

Antarctic krill have intermediate Reynolds numbers (~10^2-10^3), and how drift from oceanic features and directed movements affects their spatial distribution in this area is not well understood. In a Hudson et al. 2022, evidence was presented of a subsurface eddy that can retain simulated diel vertical migrators for up to 50 days. The presence of this feature may explain the shorter foraging trips of the penguins in this area. The presence of a nearshore, biomass dense, but spatial chaotic prey field could lessen the biological benefit of remembering forage locations. Additionally, the penguins foraged continually while out at sea, instead of focusing their efforts in bursts as ARS would predict. This could point to a lack of knowledge of dense prey locations at this day-to-day scale, or that the entire region of their foraging area is on the whole equally profitable. If the prey field is impossible to predict on small temporal and spatial scales, but stays rich in resources on the whole, a random transect-style sampling of the small area would be a sufficient foraging strategy. This again highlights the need for better understanding of the drivers of krill distributions in this general foraging area.

The rate of foraging by the penguins did not change based on the movement type in either species we tested. Bernard et al. 2017 describes three main types of krill aggregations in this region, one being “Large-dense”. These types of aggregations are shallow, biologically dense, and cover a larger area than other krill aggregation types. Another type is the “Small-close” aggregations which cover less area that the large-dense type but are deeper. From our analysis, penguins of both species seem to forage at equal rates regardless of movement type. This suggests horizontal movement strategy for the penguins in this region is not an indication of increased effort allocated. The change in horizontal movement mode from directed to resident could indicate a shift in the type of krill aggregation that the penguin has found. In the large-dense aggregations a penguin could move quickly through the area while diving and feeding on the shallower krill as it moves. If it finds a small-close aggregation which is deeper, the penguin may need to slow down its horizontal speed to reach the deeper krill. This would also explain why more time is spent by the penguin in directed modes, as the large-dense aggregations cover a larger area than the small-close aggregations.

While the possibility of the weak influence of optimized animal behavior is present, it is difficult to reject the conclusion that the animals in this region simple do not have any need to exhibit elaborate and optimized foraging strategies. Most likely this is due to the fact that within the area surrounding the Palmer Deep Canyon, the prey in this region is highly predictable and abundant on the scale of the area in which they forage. Penguins near Palmer Deep travel 5-20 km to forage while penguins of the same species in other colonies can travel 100-250 km (Ainley et al. 2015, Riaz et al. 2020). So, on a larger scale, looking at the entire range that the penguins could be foraging at, there is very tight selection for the northern edge of the Palmer Deep Canyon. If prey is consistently delivered to these colonies in an optimal way, this takes away the need for the penguins to forage in an optimal way. Krill exhibit diel vertical migration (DVM), interacting with ocean currents throughout the water column (Brierley 2014). This DVM could facilitate the retention and enhancement of zooplankton stocks in areas of high biological activity (Batchelder et al. 2002, Emsley et al. 2005). The subsurface cyclonic eddy over Palmer Deep Canyon did retain simulated krill and delivered them to them penguin foraging area just north of the canyon feature (Hudson et al. 2022). A second simulation study found that without the canyon feature present, simulated krill are delivered and retained in much lower quantities (Hudson et al. 2022). This suggests that the canyon is driving penguin foraging behavior by increasing the prey availability in the area north of the Palmer Deep Canyon. This reliable resource area could be rich enough in krill and other zooplankton that it renders the need to remember specific locations or focus on small high density krill aggregations irrelevant. If there is enough prey in the general area north of Palmer Deep throughout the breeding season, it would make sense for the penguins to reliable and continuously forage in that area. Optimal foraging theory assumes that the scarcity of resources and the high energy cost of obtaining those resources would drive animals to forage in predictable and optimized ways. However, if resources are not scarce and there is a relatively low cost to obtain them, there is no reason to expect the emergence of behavioral modes that optimize foraging success

As penguins were tagged with two types of external tags, there is the possibility of bias from instrument effects. The size of external tags has been shown to negatively affect the dive duration, dive depth, and number of dives in Adélie penguins (Ropert-Coudert et al. 2007). However, as our study focuses mainly on comparing the foraging behavior of individuals against themselves or against individuals of the same species from the same colonies with the same equipment attached, potential biases from the external tags have been minimized. Additionally, our vertical forage metrics use depth time series data that does not give direct measurement of prey consumption. Animal borne video cameras and accelerometers can provide more accurate identification of individual prey capture events, however it is difficult to gain extended datasets using these methods. In the future, as technology advances these methods should be implemented for longer term studies. At present, the methods presented here for identifying foraging from TDR data are abundant in the literature for these species (Chappell et al. 1993, Lescroël & Bost 2005, Pickett et al. 2018).

These results indicate that researchers should be wary of assuming discrete behavioral states from horizontal movement information alone, especially when the type of relocation estimates are prone to significant error. While many studies have confirmed the alignment of horizontal and vertical foraging indices in marine foragers (Dragon et al. 2012, Planque et al. 2020), others have found little overlap in areas of ARS and increased foraging intensity (Robinson et al. 2007, Weimerskirch et al 2007). The Adélie and gentoo penguins studied near Palmer Deep forage shallower and closer to shore than other species that follow seem to follow ARS effort allocation, such as southern elephant seals. This decrease in effort costs could account for a lower benefit to an optimized foraging trip. Further study is needed to parse out what factors influence the overlap of horizontal and vertical foraging intensity, whether that be distance from foraging area, prey type, or prey distribution.

By combining highly accurate GPS location data, vertical movement data, and a novel methodology, we have provided further insights into the foraging behaviors of two important marine species. Horizontal trajectory similarity was not related to vertical foraging success in either species, nor was it influenced by wind speed or tidal stage. From shuffling trajectories, we cannot reject the possibility that the penguins in this region are randomly sampling the aggregating feature associated with Palmer Deep canyon. Within this feature there may be some attraction to fine scale physical features untested in this study but the effects of those attractions would be weak if present at all. At the scale of these species' total foraging area, the circulating feature produced by the bathymetry of the region appears to be the main driver of foraging patterns, rather than optimization driven by scarcity. Both species did not modify vertical foraging rates in different horizontal movement types, but appeared to forage continuously. Marine tracking studies moving forward should be wary of assuming foraging based on purely horizontal movement type and should seek to integrate vertical and horizontal indices when possible. Additionally, this study demonstrates how deeply coupled marine organisms are to the physical features of their environment and that these features can elicit behaviors that would not be expected when using a purely organismal view. An optimal behavior could look vastly different between populations and to draw accurate conclusions even within the same species, a thorough understanding of the relevant abiotic and biotic factors is critical.

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Appendix A

LINEAR MIXED EFFECTS MODEL TABLES

Table 4 Coefficients for the linear mixed effects model for predicting Fréchet distance in Adelie penguins with wind parameters included (n = 65). Data came from 29 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	16.51	53.73	0.307	0.75990
Total Wiggles	73.05	37.42	1.952	0.05623
Vertical Dive Rate	-13329.97	13159.17	-1.013	0.31573
Season 2020-21	-998.97	1161.53	-0.860	0.40260
Colony Humble Island	-4022.37	1558.56	-2.581	0.01958
Colony Torgersen Island	-1150.87	1664.77	-0.691	0.49803
Trip 1 tidal stage -semi-diurnal	-964.69	1670.20	-0.578	0.56696
Trip1 Wind Speed	-79.36	114.02	-0.696	0.49000
Trip2 tidal stage – semi-diurnal	-612.81	1543.30	-0.397	0.69346
Trip2 wind speed	203.24	123.82	1.641	0.10707
Wind Difference	185.27	143.49	1.291	0.20412

Table 5 Coefficients for the linear mixed effect models predicting Fréchet distance in gentoo penguins including wind data (n = 32). Data came from 12 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	-153.96	303.48	-0.507	0.6170
Total Wiggles	20.89	44.18	0.473	0.6411
Vertical Dive Rate	4214.47	18348.79	0.230	0.8205
Season 2020-21	-2208.39	2569.34	-0.860	0.3993
Trip 1 tidal stage -semi-diurnal	460.36	2899.14	0.159	0.8753
Trip1 Wind Speed	-147.74	480.58	-0.307	0.7614
Trip2 tidal stage – semi-diurnal	-327.87	3607.83	-0.091	0.9284
Trip2 wind speed	-98.00	458.58	-0.214	0.8327
Wind Difference	30.65	656.55	0.047	0.9632

Table 6 Coefficients for the linear mixed effects models for predicting sum distance in Adelie penguins including wind parameters (n = 63). Data came from 29 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	444.39	2879.97	0.154	0.87775
Total Wiggles	3789.76	1981.90	1.912	0.06039
Vertical Dive Rate	-539598.56	694936.94	-0776	0.44074
Season 2020-21	-40913.18	60407.51	-0.677	0.50874
Colony Humble Island	-222118.06	79960.34	-2.778	0.01449
Colony Torgersen Island	-31383.79	88543.06	-0.354	0.72763
Trip 1 tidal stage - semi-diurnal	19890.07	96920.09	0.205	0.83781
Trip1 Wind Speed	-6844.94	6252.01	-1.095	0.27519
Trip2 tidal stage – semi-diurnal	-73320.55	85557.31	-0.857	0.39270
Trip2 wind speed	8471.83	6683.65	1.268	0.20759
Wind Difference	11678.58	7804.95	1.496	0.13591

Table 7 Coefficients for the linear mixed effects model for predicting sum distance in gentoo penguins including wind parameters (n = 31). Data comes from 12 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	-24170	19850	-1.218	0.2285
Total Wiggles	807.5	2560	0.315	0.7588
Vertical Dive Rate	652300	1075000	0.607	0.5472
Season 2020-21	-137000	145600	-0.941	0.3778
Trip 1 tidal stage - semi-diurnal	970.8	161000	0.006	0.9952
Trip1 Wind Speed	-19480	25840	-0.754	0.4558
Trip2 tidal stage – semi-diurnal	-70190	191800	-0.366	0.7179
Trip2 wind speed	4187	24600	0.170	0.8669
Wind Difference	20520	38150	0.538	0.5924

Table 8 Coefficients for the linear mixed effects model for predicting Fréchet distance in Adelie penguins with wind parameters excluded (n = 78). Data came from 31 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	7.951	49.097	0.162	0.8718
Total Wiggles	56.163	24.265	2.315	0.0236
Vertical Dive Rate	-21317.104	11375.799	-1.874	0.0656
Season 2020-21	-737.321	948.825	-0.777	0.4477
Colony Humble Island	-3573.418	1357.787	-2.632	0.0151
Colony Torgersen Island	-547.486	1467.243	-0.373	0.7122
Trip 1 tidal stage -semi-diurnal	888.932	1418.320	0.627	0.5329
Trip2 tidal stage – semi-diurnal	-1644.846	1420.329	-1.158	0.2513

Table 9 Coefficients for the linear mixed effect models predicting Fréchet distance in gentoo penguins excluding wind data (n = 34). Data came from 13 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	-153.84	247.54	-0.621	0.5395
Total Wiggles	23.86	34.92	0.683	0.5003
Vertical Dive Rate	8386.85	14953.35	0.561	0.5795
Season 2020-21	-2028.30	2046.91	-0.991	0.3305
Trip 1 tidal stage -semi-diurnal	166.15	2387.28	0.070	0.9450
Trip2 tidal stage – semi-diurnal	-365.04	2769.66	-0.132	0.8961

Table 10 Coefficients for the linear mixed effects models for predicting sum distance in Adelie penguins excluding wind parameters (n = 76). Data came from 31 individuals.

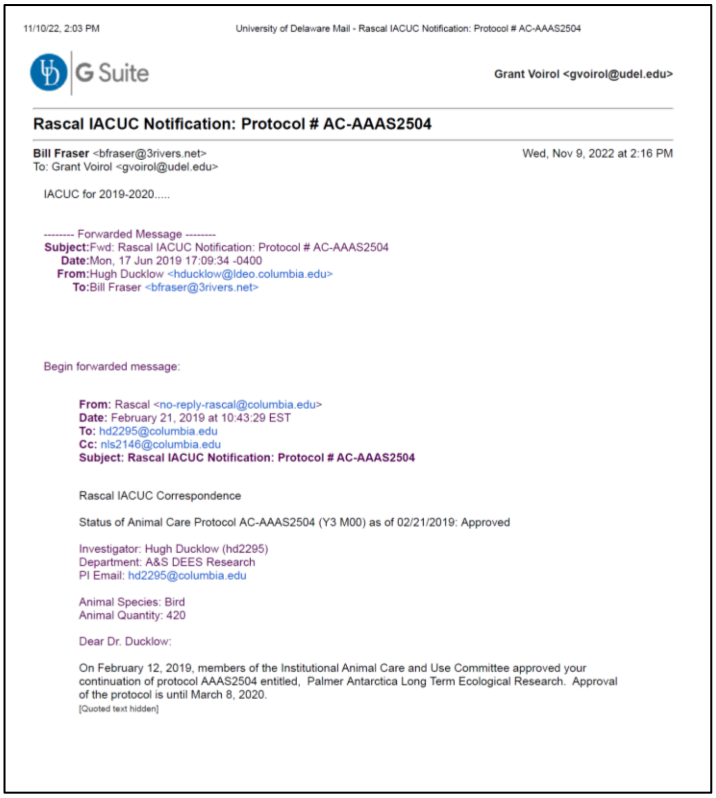
Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	306.89	2569.14	0.119	0.90507
Total Wiggles	3338.19	1246.59	2.678	0.00850
Vertical Dive Rate	-981202.03	577386.84	-1.699	0.09343
Season 2020-21	-48453.36	47849.82	-1.013	0.32371
Colony Humble Island	-200555.52	66071.57	-3.035	0.00581
Colony Torgersen Island	-9082.48	72935.16	-0.125	0.90189
Trip 1 tidal stage -semi-diurnal	91447.26	74641	1.225	0.22306
Trip2 tidal stage – semi-diurnal	-123399.46	74597.68	-1.654	0.09936

Table 11 Coefficients for the linear mixed effects model for predicting sum distance in gentoo penguins excluding wind parameters (n = 33). Data comes from 13 individuals.

Coefficient	**Estimate**	**SE**	**T value**	**P value**
Dive Frequency	-15530	13710	-1.133	0.26053
Total Wiggles	1922	1912	1.005	0.32282
Vertical Dive Rate	488700	812300	0.602	0.55007
Season 2020-21	-147100	125100	-1.176	0.26777
Trip 1 tidal stage -semi-diurnal	56420	122200	0.462	0.64496
Trip2 tidal stage – semi-diurnal	-138300	147400	-0.938	0.35304

Appendix B

IACUC



11/10/22, 2:03 PM University of Delaware Mail - Rascal IACUC Notification: Protocol # AC-AAAS2504

Grant Voirol <gvoirol@udel.edu>

Rascal IACUC Notification: Protocol # AC-AAAS2504

Bill Fraser <bfraser@3rivers.net> Wed, Nov 9, 2022 at 2:16 PM
To: Grant Voirol <gvoirol@udel.edu>

IACUC for 2019-2020.....

-------- Forwarded Message --------
Subject: Fwd: Rascal IACUC Notification: Protocol # AC-AAAS2504
Date: Mon, 17 Jun 2019 17:09:34 -0400
From: Hugh Ducklow <hducklow@ldeo.columbia.edu>
To: Bill Fraser <bfraser@3rivers.net>

Begin forwarded message:

From: Rascal <no-reply-rascal@columbia.edu>
Date: February 21, 2019 at 10:43:29 EST
To: hd2295@columbia.edu
Cc: nls2146@columbia.edu
Subject: Rascal IACUC Notification: Protocol # AC-AAAS2504

Rascal IACUC Correspondence

Status of Animal Care Protocol AC-AAAS2504 (Y3 M00) as of 02/21/2019: Approved

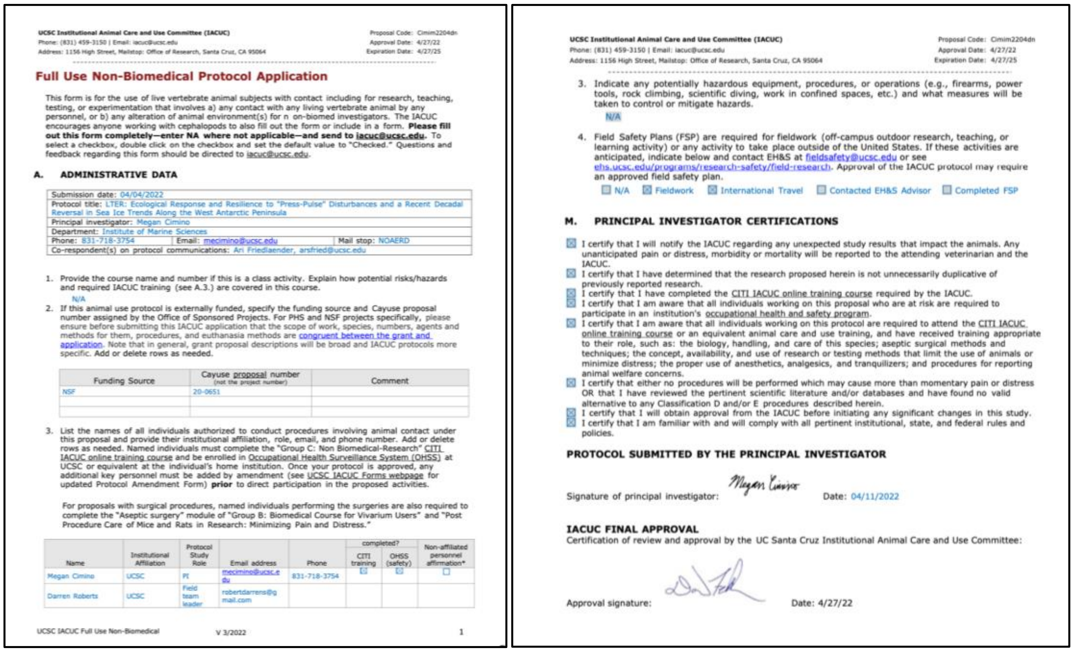
Investigator: Hugh Ducklow (hd2295)
Department: A&S DEES Research
PI Email: hd2295@columbia.edu

Animal Species: Bird
Animal Quantity: 420

Dear Dr. Ducklow:

On February 12, 2019, members of the Institutional Animal Care and Use Committee approved your continuation of protocol AAAS2504 entitled, Palmer Antarctica Long Term Ecological Research. Approval of the protocol is until March 8, 2020.
[Quoted text hidden]

Figure 9 Columbia University IACUC Approval notification. Approval is for the first year of the study.



UCSC Institutional Animal Care and Use Committee (IACUC)
Phone: (831) 459-3150 | Email: iacuc@ucsc.edu
Address: 1156 High Street, Mailstop: Office of Research, Santa Cruz, CA 95064

Proposal Code: Cimim2204dn
Approval Date: 4/27/22
Expiration Date: 4/27/25

Full Use Non-Biomedical Protocol Application

This form is for the use of live vertebrate animal subjects with contact including for research, teaching, testing, or experimentation that involves a) any contact with any living vertebrate animal by any personnel, or b) any alteration of animal environment(s) for n on-biomed investigators. The IACUC encourages anyone working with cephalopods to also fill out the form or include in a form. **Please fill out this form completely—enter NA where not applicable—and send to iacuc@ucsc.edu.** To select a checkbox, double click on the checkbox and set the default value to "Checked." Questions and feedback regarding this form should be directed to iacuc@ucsc.edu.

A. ADMINISTRATIVE DATA

Submission date: 04/04/2022		
Protocol title: LTER: Ecological Response and Resilience to "Press-Pulse" Disturbances and a Recent Decadal Reversal in Sea Ice Trends Along the West Antarctic Peninsula		
Principal investigator: Megan Cimino		
Department: Institute of Marine Sciences		
Phone: 831-718-3754	Email: mecimino@ucsc.edu	Mail stop: NOAERD
Co-respondent(s) on protocol communications: Ari Friedlaender, arsfried@ucsc.edu		

1. Provide the course name and number if this is a class activity. Explain how potential risks/hazards and required IACUC training (see A.3.) are covered in this course.

   N/A

2. If this animal use protocol is externally funded, specify the funding source and Cayuse proposal number assigned by the Office of Sponsored Projects. For PHS and NSF projects specifically, please ensure before submitting this IACUC application that the scope of work, species, numbers, agents and methods for them, procedures, and euthanasia methods are congruent between the grant and application. Note that in general, grant proposal descriptions will be broad and IACUC protocols more specific. Add or delete rows as needed.

Funding Source	Cayuse proposal number (not the project number)	Comment
NSF	20-0651	

3. List the names of all individuals authorized to conduct procedures involving animal contact under this proposal and provide their institutional affiliation, role, email, and phone number. Add or delete rows as needed. Named individuals must complete the "Group C: Non Biomedical-Research" CITI IACUC online training course and be enrolled in Occupational Health Surveillance System (OHSS) at UCSC or equivalent at the individual's home institution. Once your protocol is approved, any additional key personnel must be added by amendment (see UCSC IACUC Forms webpage for updated Protocol Amendment Form) **prior** to direct participation in the proposed activities.

   For proposals with surgical procedures, named individuals performing the surgeries are also required to complete the "Aseptic surgery" module of "Group B: Biomedical Course for Vivarium Users" and "Post Procedure Care of Mice and Rats in Research: Minimizing Pain and Distress."

Name	Institutional Affiliation	Protocol Study Role	Email address	Phone	completed?		Non-affiliated personnel affirmation*
					CITI training	OHSS (safety)	
Megan Cimino	UCSC	PI	mecimino@ucsc.edu	831-718-3754	☒	☒	☐
Darren Roberts	UCSC	Field team leader	robertdarrens@gmail.com				

UCSC IACUC Full Use Non-Biomedical V 3/2022 1

UCSC Institutional Animal Care and Use Committee (IACUC)
Phone: (831) 459-3150 | Email: iacuc@ucsc.edu
Address: 1156 High Street, Mailstop: Office of Research, Santa Cruz, CA 95064

Proposal Code: Cimim2204dn
Approval Date: 4/27/22
Expiration Date: 4/27/25

3. Indicate any potentially hazardous equipment, procedures, or operations (e.g., firearms, power tools, rock climbing, scientific diving, work in confined spaces, etc.) and what measures will be taken to control or mitigate hazards.

   N/A

4. Field Safety Plans (FSP) are required for fieldwork (off-campus outdoor research, teaching, or learning activity) or any activity to take place outside of the United States. If these activities are anticipated, indicate below and contact EH&S at fieldsafety@ucsc.edu or see ehs.ucsc.edu/programs/research-safety/field-research. Approval of the IACUC protocol may require an approved field safety plan.

   ☐ N/A ☒ Fieldwork ☒ International Travel ☐ Contacted EH&S Advisor ☐ Completed FSP

M. PRINCIPAL INVESTIGATOR CERTIFICATIONS

- ☒ I certify that I will notify the IACUC regarding any unexpected study results that impact the animals. Any unanticipated pain or distress, morbidity or mortality will be reported to the attending veterinarian and the IACUC.
- ☒ I certify that I have determined that the research proposed herein is not unnecessarily duplicative of previously reported research.
- ☒ I certify that I have completed the CITI IACUC online training course required by the IACUC.
- ☒ I certify that I am aware that all individuals working on this proposal who are at risk are required to participate in an institution's occupational health and safety program.
- ☒ I certify that I am aware that all individuals working on this protocol are required to attend the CITI IACUC online training course or an equivalent animal care and use training, and have received training appropriate to their role, such as: the biology, handling, and care of this species; aseptic surgical methods and techniques; the concept, availability, and use of research or testing methods that limit the use of animals or minimize distress; the proper use of anesthetics, analgesics, and tranquilizers; and procedures for reporting animal welfare concerns.
- ☒ I certify that either no procedures will be performed which may cause more than momentary pain or distress OR that I have reviewed the pertinent scientific literature and/or databases and have found no valid alternative to any Classification D and/or E procedures described herein.
- ☒ I certify that I will obtain approval from the IACUC before initiating any significant changes in this study.
- ☒ I certify that I am familiar with and will comply with all pertinent institutional, state, and federal rules and policies.

PROTOCOL SUBMITTED BY THE PRINCIPAL INVESTIGATOR

Signature of principal investigator: Megan Cimino Date: 04/11/2022

IACUC FINAL APPROVAL
Certification of review and approval by the UC Santa Cruz Institutional Animal Care and Use Committee:

Approval signature: Date: 4/27/22

Figure 10 University of California Santa Cruz IACUC Approval for the second year of the study.